Cognitive conflicts in the Stroop paradigm: Information retrieval and response selection in the human cognitive system

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In unserem Alltag ist kognitive Kontrolle lebensnotwendig. Sie wird benötigt, um Handlungen zu planen und diese umzusetzen. Stellen Sie sich beispielsweise vor, Sie lesen diesen Satz und gleichzeitig klopft jemand an Ihre Tür. Sie können nun entweder das Klopfen ignorieren und weiterlesen oder Sie gehen zur Tür. Sie müssen sich also entscheiden, ob Sie Ihre bisherige Tätigkeit weiterverfolgen oder ob Sie sich ein neues Ziel setzen. Kognitive Kontrolle wird besonders in solchen Momenten deutlich, wenn eine geplante Handlung gestört wird. Weil zwei widerstreitende Verhaltenstendenzen gleichzeitig bestehen oder anlaufen, entsteht ein Konflikt. Meist geschieht dies unbewusst.

Experimentell können kognitive Konflikte beispielsweise mit dem Stroop-Paradigma hergestellt werden (Stroop,1935). In der ursprünglichen Version des Stroop-Paradigmas muss die Farbe von Farbwörtern benannt werden, während die Bedeutung des Farbwortes ignoriert wird. Beispielweise wird das Farbwort BLAU dargeboten, das in roter Farbe geschrieben ist, die Farbe „rot“ wird benannt. Wenn die Farbe des Farbwortes und die Bedeutung des Farbwortes nicht übereinstimmen, ist die Benennung der Farbe erschwert. In diesem Fall wird die relevante Information, nämlich die Farbe des Wortes, durch die irrelevante Information, also das Farbwort selbst, gestört. Der Konflikt zeigt sich an verlangsamten Reaktionszeiten.

Dabei ist fraglich, ob der kognitive Konflikt zwischen der relevanten und der irrelevanten Information dann auftritt, wenn die Information wahrgenommen und verarbeitet wird oder erst dann, wenn die Antwort gegeben werden muss. Diese Frage wurde bereits mit vielen verschiedenen Stroop-Varianten untersucht. Daraus ergab sich die nachfolgende Fragestellung, ob, wie und warum sich die Ergebnisse für verschiedene Stroop-Varianten unterscheiden (Van Maanen, Van Rijn, & Borst, 2009). In der vorliegenden Arbeit werden die Fragen systematisch mit zwei verschiedenen Stroop-Varianten untersucht: Im Bild-Wort Interferenz Paradigma werden Bilder von Objekten benannt. Gleichzeitig dargebotene Wörter, die ähnliche, andere oder dasselbe Objekt bezeichnen, müssen dabei ignoriert werden. Das zu ignorierende Wort wird dabei als Distraktor bezeichnet und die intendierte Antwort als Target. Beispielsweise wird als Target das Bild von einem „Schaf“ dargeboten und muss benannt werden. Das gleichzeitig als Distraktor dargebotene Wort kann etwa ein Kohyponym des Bildnamens sein (z.B. „Ziege“), ein neutrales Wort sein (z.B. „Komet“) oder das Bild bezeichnen („Schaf“).
In der vorliegenden Arbeit werden die Ergebnisse vom Bild-Wort Interferenz Paradigma mit denen eines Zahlenstroop verglichen. Bei dem Zahlenstroop werden Zahlworte gezählt. Es wird also beispielsweise „Zwei Zwei Zwei“ dargeboten. Die Anzahl der Wörter wird benannt und das Wort selbst ignoriert. In diesem Fall wäre das Target „drei“, das Zahlwort „Zwei“ fungiert als Distraktor. Wie im Bild-Wort Interferenz Paradigma, wird auch beim Zahlenstroop die Nähe zwischen Target und Distraktor systematisch variiert. Beide sind entweder verwandt („Zwei Zwei Zwei“), neutral („Mann Mann Mann“) oder identisch („Zwei Zwei“).

Ausgehend von der bisherigen Forschung mit verschiedenen Stroop-Paradigmen wird angenommen, dass die Benennung des Target am schwierigsten ist, wenn Target und Distraktor verwandt oder „relatiert“ sind, besonders, wenn sie Kohyponyme sind (Schriefers, Meyer, & Levelt, 1990). Wenn Target und Distraktor jedoch identisch sind, ist die Benennung üblicherweise beschleunigt (MacLeod, 1991). Der Konflikt zwischen der relatierten und der neutralen Bedingung wird als Interferenzeffekt bezeichnet. Der Interferenzeffekt soll den Konflikt festhalten, der durch die semantische Nähe zwischen Target und Distraktor entsteht. Im Gegensatz dazu wird der Stroopeffekt durch den Vergleich der relatierten mit der identischen Bedingung ermittelt. Damit soll gemessen werden, welche Verarbeitungsschwierigkeit relatierte Distraktoren generell hervorrufen.
Um herauszufinden, wann und wo die Konflikte zwischen dem Target und dem Distraktor stattfinden, wurden in der vorliegenden Arbeit mit beiden Stroop-Varianten Reaktionszeitexperimente und fMRT-Experimente durchgeführt. Dabei zeigte sich, dass in beiden Paradigmen relatierte Distraktoren tatsächlich zu kognitiven Konflikten führen, was sich in verlangsamten Reaktionszeiten zeigt. Diese Reaktionszeitunterschiede verschwinden jedoch, wenn Target und Distraktor nicht gleichzeitig, sondern nacheinander dargeboten werden. Daraus wurde geschlossen, dass die Konflikte in beiden Paradigmen bei der Verarbeitung der Stimuli auftreten und nicht erst bei der Antwortauswahl (vgl. Janssen, Schirm, Mahon, & Caramazza, 2008). Obwohl der Interferenzeffekt und der Stroopeffekt in beiden Paradigmen große Ähnlichkeit in ihrem zeitlichen Ablauf aufwiesen, zeigten sich jedoch neuronal große Unterschiede. Während sich der Interferenzeffekt im Bild-Wort Interferenz Paradigma linkshemisphärisch zeigte, wurde der Effekt im Zahlenstroop rechtshemisphärisch verarbeitet. Außerdem zeigte sich neuronal im Bild-Wort Interferenz Paradigma sowohl beim Abruf als auch bei der Antwortauswahl ein starker Stroopeffekt, der im Zahlenstroop nicht auftrat. Im Gegensatz dazu gibt es Hinweise darauf, dass im Zahlenstroop besonders dann starke Verarbeitungsschwierigkeiten auftraten, wenn Target und Distraktor identisch waren.

Die Ergebnisse sprechen dafür, dass der Interferenzeffekt in beiden Paradigmen zwar zu demselben Zeitpunkt stattfindet, nämlich beim Abruf und bei der Verarbeitung der Information und nicht bei der Antwortauswahl, jedoch liegen ihnen neuronal unterschiedliche Prozesse zugrunde. Auch für den Stroopeffekt legten die Reaktionszeiten nahe, dass die Konflikte in beiden Paradigmen eine große Ähnlichkeit in ihrem zeitlichen Verlauf aufweisen. Neuronal scheinen sich die Prozesse jedoch stark zu unterscheiden.

Contents

Chapter 1

Introduction

In daily life, we constantly have to adjust our goals and plans to changing task demands and internal needs. For instance, while reading this sentence, you might get distracted by somebody knocking on your door or by feeling thirsty. In this case, you have to decide whether you stop what you're doing or stay on the task and block yourself off from the distraction. Therefore, to perform a successful task, we have to balance the initiation and inhibition of our actions. This becomes particularly clear when a predominant impulse must be suppressed in favour of an appropriate response. Our ability to solve such a conflict is referred to as cognitive control.

To study the processes of cognitive control, the Stroop Paradigm has become a popular tool (Stroop, 1935). Its original finding was that naming the ink colour of a word is severely hindered when the word refers to another colour, for example, naming the ink colour of the word RED printed in blue. In this task, compared to, for example, naming the colour of a patch, reaction times and error rates are strongly increased. These costs, i.e. the decreased performance due to the irrelevant colour word – henceforth referred to as distractor – have been taken as a direct measure for the amount of cognitive control needed to suppress the unsolicited response.

The Stroop Paradigm is frequently used to address central questions of cognitive control. It is, for instance, an open issue, where and when in the processing stream cognitive conflicts arise. Do they arise early, for example, during the retrieval of target and distractor? Or do they occur late, when the response is prepared for execution? Another debate is concerned with the question whether the findings agree for different Stroop variants (Van Maanen et al., 2009).

In this dissertation I present research on the temporal characteristics and the neural substrates of cognitive conflicts during the processing of objects and numbers. To better understand the locus of the conflict, the retrieval phase and the response phase are modelled separately. To examine the conflicts' particular nature, I'll compare similarities and differences in the conflict processing of distinct core systems (objects and numbers).

I propose the hypothesis that processing costs occur during retrieval, therefore, early in the processing stream, for both – object and number representations. I further propose that the resolution of the conflict between target and distractor for number and object representations does not rely on common neural substrates. I will present results from behavioural and functional imaging experiments, showing similar temporal patterns for the conflicts in both systems, but distinct underlying neural networks.

According to Spelke (2000, 2003), objects and numbers are processed in different core systems. In Chapter 2, I will present an overview on the cognitive processes and the neural substrates regarding these systems. The core system of *number representation* is proposed to process imprecise and abstract magnitudes (Chapter 2.1), the core system of *object representation* is assumed to be specified in the identification of object boundaries (Chapter 2.2). All core knowledge systems are suggested to be encapsulated and to originate early in human ontogeny, however, with development, human beings seem to be able to combine the systems with language (Spelke, 2003). Because language plays a crucial role in the representation of the core systems in human adults, and apart from that, speech production was essential to perform the naming procedure in the Stroop Paradigms, Chapter 3 will be dedicated to the cognitive stages and neural substrates of speech processing, in particular, single word production. Chapter 4 will introduce the Stroop paradigm as a measurement for cognitive conflict, with a focus on the two variants used in the present study, namely, first, a Stroop with numbers and, second, a Stroop with objects, which is also commonly known as *Picture-Word Interference paradigm* (W. Glaser & Düngelhoff, 1984; Schriefers et al., 1990). In Chapters 5 and 6, I will present the results of the experiments, which I con-

ducted in order to test my hypotheses. Chapter 5 is dedicated to the reaction time studies and Chapter 6 to the functional imaging experiments of both paradigms. Both chapters will contain a discussion of its corresponding results. Finally, in the Discussion, Chapter 7, I will compare the results of the behavioural and the functional imaging studies.

The underlying architecture of the cognitive and neural processes which implement cognitive conflicts is key to debates about the nature of cognitive control.

The particular tasks I focus on here are two variants of the Stroop task (Stroop, 1935). By manipulating input and output elements of the task independently I hope to shed light on the issue of *retrieval* versus *response* processing.

Even though Stroop tasks are frequently investigated, the theoretical and empirical debate concerning the source of conflict remains. For example, some suggest that conflicts in the Colour Stroop Paradigm arise either from perceptual or semantic input effects (Luo, 1999; Sturz, Green, Locker Jr, & Boyer, 2013; Seymour, 1977), from response output effects (Fagot & Pashler, 1992; Dell'Acqua, Job, Peressotti, & Pascali, 2007; Van Maanen & Van Rijn, 2008; Van Maanen et al., 2009) or a combination of both (De Houwer, 2003; Chen, Lei, Ding, Li, & Chen, 2013; Schmidt & Cheesman, 2005; Zhang & Kornblum, 1998).

Similarly, the locus of the conflict in another Stroop variant, namely the Picture-Word Interference paradigm, has been the matter of an extensive debate: Again, its source is either attributed to the retrieval stage (Aristei & Abdel Rahman, 2013; Levelt, Roelofs, & Meyer, 1999; Roelofs, 1992, 1997; Roelofs & Piai, 2013; Schriefers et al., 1990), to the response stage (Dhooge & Hartsuiker, 2010, 2011; Finkbeiner & Caramazza, 2006; Janssen et al., 2008; Mahon, Costa, Peterson, Vargas, & Caramazza, 2007), or a combination of the two (Goldrick, Dell, Kroll, & Rapp, 2009).

Although examinations on both tasks have yielded many convergent results, the findings are typically interpreted in the context of different models: The findings from the Colour Stroop task have been discussed in the context of cognitive control and attention allocation, the Picture-Word Interference paradigm, on the other hand, has mostly been used to investigate the sequence of processing stages in word production. Also the Numerical Stroop task has been used to examine the locus of the conflict, and specific questions regarding numerical processing.

However, as mentioned, few researchers have argued that conflicts in the Colour-Stroop task and the Picture-Word Interference paradigm both reflect semantic competition during the retrieval phase. Therefore, semantic similarity between the relevant and the irrelevant dimension of the Stroop stimuli in both paradigms is suggested to determine the amount of interference (Luo, 1999; Seymour, 1977). To be able to dissociate semantic competition effects in the Stroop paradigm and the Picture-Word Interference paradigm, in the present study, rather than the Colour-Stroop task, a Numerical Stroop task was used. The Numerical Stroop task was expected to have several advantages: First, it was supposed to elicit numerical instead of semantic conflicts. Second, the Picture-Word Interference task and the Numerical Stroop task were supposed to be located in separate core systems and therefore expected to depict conflicts in distinct cognitive systems. Third, with using number stimuli I assumed to be able to quantify the numerical proximity between the relevant and the irrelevant numerical dimension; a closer proximity was expected to cause stronger interference effects (numerical distance effect; Moyer & Landauer, 1967).

Consequently, the aim of the present study is twofold. First, I'll address the issue of the temporal locus of conflicts in naming tasks. Second, I aim to contribute to the debate on whether or not conflicts in the Picture-Word Interference task and in the Stroop task are 'two sides of the same coin' (Van Maanen et al., 2009), by comparing two Stroop-like paradigms, which are identical in their formal structure and show a close resemblance in their conflict factors, but differ fundamentally regarding their underlying cognitive processes. In particular, I chose to compare tasks which are based in different core systems, namely the number core system and the object core system. To do so, I'll conduct a Numerical Stroop paradigm (NSP) and a Picture-Word Interference task (PWI).

In the Picture-Word Interference task (PWI), participants have to name the picture of an object, i.e. the picture of a *dog*, which is coupled with a task-irrelevant distractor word. The word and the picture can either be related (e.g. 'cat'), unrelated (e.g. 'hat') or identical (e.g. 'dog'). (For a review on this task, see Chapter 4.1.2 *Object Stroop*.)

In the Number Stroop paradigm (NSP), participants have to count words, and the meaning of the word is, again, task-irrelevant. The quantity of the word(s) is either from the same domain, but incongruent (e.g. 'four four four'), from a different domain and thus unrelated (e.g. 'man man man') or identical with the words' meaning (e.g. 'four four four four') (See Chapter 4.1.1 *Number Stroop*).

Following the convention in literature (e.g. Roelofs, 2003), I'll refer to the contrast between the related

and unrelated condition (PWI) or the incongruent and unrelated condition (NSP) as *Interference effect*, and the contrast between the related and identical condition (PWI) or the incongruent and identical condition (NSP) as *Stroop effect*.

Accordingly, both paradigms follow the prototypical Stroop procedure, in particular, naming a target while ignoring task-irrelevant information, which is either closely associated (related/incongruent condition), unrelated or identical with the task. The Interference effect is supposed to depict the influence of the relatedness of target and distractor; the Stroop effect is assumed to reflect the mere exposure to a task-irrelevant distractor word.

However, in the PWI, objects are perceived and conceptualized and the semantically related distractor word is expected to compete with the name of the target object. In the NSP, on the other hand, numbers are counted, and the numerically related number word is expected to interfere with the processing of the quantity. With this approach I'll be able to pinpoint Interference and Stroop effects in different core systems and to identify similarities and differences in the conflict processing across tasks.

Historically, Stroop tasks have been analysed behaviourally with reaction times (RTs; for a review on the Stroop effect, see MacLeod, 1991), while varying the semantic proximity between target and distractor (e.g. G. Klein, 1964) or manipulating the stimulus onset asynchrony (SOA; e.g. M. O. Glaser & Glaser, 1982; De Houwer, 2003; Luo, 1999). Recently, psychophysiological methods, such as EEG (e.g. Appelbaum, Meyerhoff, & Woldorff, 2009; Coderre, Conklin, & van Heuven, 2011; Hanslmayr et al., 2008), fMRI and PET (for a review, see Cieslik, Mueller, Eickhoff, Langner, & Eickhoff, 2015) have been used to delineate the corresponding brain regions.

Stimulus onset asynchrony (SOA) refers to the time interval between target and distractor onset. SOA manipulations allow to distinguish between input and output effects and to assess the different stages in the cognitive process. If the relevant and the irrelevant dimension are displayed simultaneously, both interfere, especially when the to-be-ignored dimension (e.g. the colour word) is processed faster. Typically, strong interference effects are still present in a time window of $\pm$100 ms around simultaneous, but with increasing distractor pre- or postexposure, i.e. at long SOAs, interference effects tend to decrease (Dyer, 1971; M. O. Glaser & Glaser, 1982). However, manipulating SOA has no effect on word reading. These findings have challenged the idea that the only determinant of the conflict is the arrival time of the two dimensions at the response stage (*response competition hypothesis*), because in this particular case, one should be able to find a SOA which compensates for the slower processing of the colour. At this SOA, interference effects for word reading and colour naming should be equivalent (M. O. Glaser & Glaser, 1982; MacLeod, 1991). There is no evidence for that.

However, in some studies, interference effects have been reported at a long SOA, in other words, even if the slower dimension was given a head start, RTs were still increased in the context of the irrelevant distractor word, which is interpreted to indicate response competition (e.g. Janssen et al., 2008). This is assumed because the participant is expected to have ample time to retrieve the name of the target before the distractor appears, consequently, both dimensions are expected not to compete at the retrieval phase.

Also in the present study (Chapter 5), a similar SOA manipulation will be used to examine the locus of the conflict. Because processing costs are expected to occur during retrieval, interference effects are supposed to be observed in the context of immediate naming, but not delayed naming tasks. According to the usual practice, in the immediate naming task, target and distractor are presented simultaneously. In the delayed task, the response is postponed until a cue is shown, and naming latencies are measured from cue onset. Because the retrieval phase is expected to be terminated by then, possible effects are supposed to reflect 'late' response conflicts.

However, with only one behavioural measure, the source of the conflict cannot be located directly. Instead, it must be deduced from the naming latencies. As a consequence, I'll use fMRI experiments (see Chapter 6), which allow me to separately model the BOLD response associated with the retrieval and the response selection processes. I aim to identify brain networks, in which activation is modulated by either task or response conflicts. For each time period and task, different brain areas are supposed to reflect an increased cognitive demand: during the counting procedure of the NSP, conflicts are expected to elicit enhanced activity in the bilateral horizontal segment of the intraparietal sulcus (hIPS) (Dehaene et al., 2003). During the retrieval phase of the PWI, on the other hand, competing lexical items are supposed correlate with the BOLD signal in the left middle temporal gyrus (Indefrey, 2011) and left inferior frontal gyrus (Price, 2012). And in both tasks, response conflicts are expected to manifest in key regions for supervisory attentional control, which are mainly located at the inferior frontal junction (Brass et al., 2005) and in the anterior cingulate cortex (Botvinick, 2007).

Chapter 2

Core Systems

According to Spelke (2000); Spelke and Tsivkin (2001); Spelke (2003); Spelke and Kinzler (2007), human beings are endowed neither with a single, general-purpose learning system nor with various special-purpose systems, but with four or five flexible systems of core knowledge, which are proposed to represent *objects*, *numbers*, *agents*, *space*, and, possibly, *social partners*.

The present study is based on two of these core knowledge systems: The number system is represented by a task in which number words are counted, whereas the object system is investigated with a task in which pictorial objects are named.

The system of object representation is supposed to be specified in inanimate entities, which are bounded as whole, and their distinctive movements. In a separate system, sets and their numerical relations may be ordered, added and subtracted. Agent representations are defined by their goal-directed actions, by their efficiency, contingency, and gaze-direction. In the space core system the geometry of the environment is captured. And the core system for social partners may rely on their cooperation, reciprocity and group cohesion. Hence, each system is provided with a set of principles which serve to individuate its particular properties (Spelke & Kinzler, 2007).

All core knowledge systems are proposed to originate early in human ontogeny and phylogeny, and may thus be identified across task, age, human culture, and even across species.

The systems are considered to be domain-specific, encapsulated and isolated. However, with development, human beings are supposed to be able to combine different core systems, that is, with language: "Natural languages provide humans with a unique system for combining flexibly the representations they share with other animals" (Spelke, 2003, p. 291). The outstanding flexibility of human beings is thus assumed to originate in their ability to connect the core foundations, serving to develop new skills and beliefs.

The core system of **number representation** is considered to be specified in the processing of numerical magnitudes. It is believed that number representations are imprecise, abstract, comparable and combinable. The *imprecision* of number is ratio-dependent and increasing with numerical magnitudes. Number representations are *abstract*, that is, independent of modality, and may thus be applied to all kinds of objects, sounds, and sequences of actions. Numerical representations can be *compared*, and *combined* with basic operations like addition and subtraction (Feigenson, Dehaene, & Spelke, 2004; Spelke & Kinzler, 2007).

Basic numerical abilities have been demonstrated not only for human adults across cultures but also for pre-verbal infants and for various animal species like apes, monkeys, pigeons, lions, and also for salamanders and bees (Gallistel & Gelman, 1992, 2000; Dehaene, Molko, Cohen, & Wilson, 2004; Dehaene, 2011; McComb, Packer, & Pusey, 1994; Nieder, Freedman, & Miller, 2002). Even neonates with a mean age of 49 hours, who are familiarized to a multisyllabic stream, are reported to be able to match the respective number of syllables to a set of visually presented objects (Izard, Sann, Spelke, & Streri, 2009). And Mehler and Bever (1967) discovered that two-year old infants, who were offered to choose a row of M&M candies, were able to select the larger of two amounts, even if the numerosity conflicted with row length. "Occasionally children responded one way on verbal judgements on which clay row had 'more', yet in the case of M&M's they took the other row to eat" (Mehler & Bever, 1967, p. 2). The assumption of domain-specificity of quantity-representations is also supported by a case study of the neurological patient I.H., who suffered from semantic dementia and whose language comprehension and production abilities were severely impaired. However, he still mastered various numerical tasks, like

cardinality judgement and dot pattern seriations, counting, numerosity seriation, transcoding numerical symbols to other formats (Arabic numerals to number words and vice versa, either written or spoken), he could place numbers on a number line and he was good in all kinds of single digit (e.g. $1 + 8$) and multi-digit calculation operations (e.g. $742 - 393$) (Cappelletti, Butterworth, & Kopelman, 2001).

The prediction that basic numerical abilities are non-verbal and present across cultures, is supported by a study on the Amazonian tribe Mundurukú (Pica, Lemer, Izard, & Dehaene, 2004). The Mundurukú only have words for the numbers from one to four, for five ('one hand'), ten ('two hands'), for 'some' and 'many'. Nevertheless, they seem to be able to estimate and compare sets of items and to perform approximate addition and subtraction just as well as a control group of French adults, but they fail in exact subtraction tasks. The findings are interpreted to suggest the presence of a non-verbal system for number approximation, which may be distinguishable from a separate, language-based counting system for exact number and arithmetic (Pica et al., 2004).

Recently, Feigenson et al. (2004) have suggested to subdivide the number core system into a 'first number core system' for the representation of small and exact quantities and a 'second number core system' for the representation of large and approximate numerosities. Both core systems are supposed to account for our basic numerical abilities, and may serve as a fundament for more sophisticated numerical faculties that are uniquely human.

The core system of **object representation** is specified in the perception of object boundaries. It enables us to sense objects even if they are moving or in case they are partly or fully out of view. There are three spatio-temporal principles which support the perception of objects, these are: cohesion, continuity and contact. *Cohesion* refers to the characteristic of an object to move as a whole, *continuity* describes the steadiness of its movement, and *contact* predicates the object's inability to interact at a distance (Spelke, 2003).

The presupposition of coherence seems to be observable in humans and animals, even if they do not have any prior visual experience, for instance, in human infants and newly hatched chickens. The behaviour of the chicks was investigated by Regolin and Vallortigara (1995). Only a few hours after they hatched, they were imprinted to a red triangle, which was partly occluded by a rod. On their third day, the chicks were transferred to a new cage and provided with the option to either approach a complete or a fragmented triangle. (The size of the red area was controlled in a separate experiment.) The chicks preference to approach the solid triangle was interpreted as evidence for their ability to represent the continuous existence of an object. Similarly, the concept of individual entities plays a prominent role in the object perception of five-month-old infants: In a preferential looking paradigm by Wynn (1992), for instance, infants were confronted with a puppet, which was subsequently hidden behind a screen. A second puppet approached the same screen and was hidden behind it. Even though the infants had only seen one puppet at a time, they looked longer at a screen which revealed only one puppet, indicating that they had expected to see two.

The object core system is proposed to be limited to a small number, presumably three to four entities for adults and two to three items for infants (Coubart, Izard, Spelke, Marie, & Streri, 2014; Gallistel & Gelman, 1992; Feigenson et al., 2004). Adults are reported to not be able to track moving objects, if their number exceeds the respective set limit or if one of the spatio-temporal principles is violated (Spelke & Kinzler, 2007).

2.1 Numbers

The representation of magnitude is frequently investigated with numerical comparison studies. In an influential study by Moyer and Landauer (1967), participants had to decide which of two presented single digits was numerically larger. Subjects responded quicker and more accurately if the digits were further apart (e.g. 1 and 9) than if they were closer together (e.g. 1 and 2). This finding was interpreted to reflect an internal, analogous representation for magnitude, similar to a physical continuum, on which numbers with small distances may overlap. In addition to the *numerical distance effect*, also a *size* - or *ratio effect* was found: at equal numerical distance, two quantities were more easily discerned as their numerical magnitude decreased. For instance, 1 and 2 were easier to discriminate than 8 and 9, which was explained by their ratio. The correlation between the ratio and the reaction time (RT) was even stronger than the correlation between the absolute distance and the RTs (Moyer & Landauer, 1967).

Both distance and ratio have been used as independent variables in various studies to investigate whether the representation of numerical magnitudes can best be described as a function of linear or logarithmic models. Gallistel and Gelman (2000), for instance, argue in favour of a linear mental number

line, whereas Dehaene, Bossini, and Giraux (1993) follow Moyer and Landauer's suggestion (1967) of a logarithmically compressed mental number line, corresponding to the Weber-Fechner law. An alternative view was suggested by Siegler and Opfer (2003); according to them, the mental representation may change gradually from logarithmic to linear with increasing age. In their study, preschoolers and adults had to determine the spatial position of a given number on a hypothetical number line.

Early neuroscientific research used ERP studies to investigate how numerical distance affects the neuronal time course. Dehaene (1996) conducted a study that focused on a number comparison task with digits and number words. The subjects were instructed to judge whether a presented digit or number word was larger or smaller than the reference number '5'. Dehaene (1996) found an initial notation effect (N1), with a left hemispheric dominance for verbal stimuli (146 ms post-stimulus), but bilateral for digits (160 ms post-stimulus). A posterior positivity (p2P) was interpreted to reflect numerical distance representations for digits (174 ms post-stimulus onset), peaking later for verbal stimuli (196 ms post-onset), which was consistent with the reaction time data. These findings were interpreted to show, first, a left-lateralized and early visual decoding for verbal stimuli. Second, a notation-independent magnitude representation in the inferior parietal cortex is suggested, possibly with a right hemispheric dominance.

These findings were integrated in the early *triple code model* of numerical processing, in which an a-modal magnitude representation was distinguished from arabic and verbal representations (Dehaene & Cohen, 1996). Meanwhile (2004), this tripartite distinction has been specified both anatomically and functionally.

2.1.1 Neural Core System of Number Processing

Recent neuroscientific research has identified a number of brain regions concordant among studies that used numerical cognition, i.e. involving numbers and arithmetic tasks. Especially the bilateral inferior parietal lobes but also frontal regions are considered to play a crucial role in the processing of numbers.

Arguably in particular intraparietal regions or more precisely the *horizontal segment of the intraparietal sulcus* (hIPS) plays a pivotal role in the processing of an abstract, plurimodal representation of number (Arsalidou & Taylor, 2011; Dehaene et al., 2003, 2004; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Cohen Kadosh et al., 2005).

Dehaene et al. (2003, 2004) claim that the hIPS might serve as a neural circuit to a 'core quantity system', and it is presumed to act analogously to a spatial map or mental number line. The hIPS is found active whenever mental arithmetic such as addition and subtraction is performed. It is activated for the estimation of approximate results of such calculations, for number comparisons, it assumed to be sensitive to numerical magnitude and presumably even to unconscious numerical processing.

In a functional imaging meta-analysis across various arithmetic tasks by Arsalidou and Taylor (2011), general numerical processing was associated with a set of brain areas, mainly in the parietal lobes in both hemispheres, in particular in superior and inferior parietal regions, but also frontal and cingulate activity was observed. Addition, subtraction and multiplication tasks differentially recruited the left and right hemispheres in the parietal cortex (Brodmann areas 7 and 40). Whereas addition and subtraction were processed dominantly in the left hemisphere, activity for multiplication was right-lateralized.

The hIPS seems to be active whenever a comparative operation needs access to a numerical scale, furthermore, it is assumed to be responsive to numerical distance (Piazza & Dehaene, 2008; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Pinel, Piazza, Le Bihan, & Dehaene, 2004).

For example, in a study by Pinel et al. (2004), comparative judgements on the magnitude of digits and on the physical size and luminance of digits and letters were made. Enhanced activity in the bilateral hIPS was observed for number-size interference across task and notation. The interference of luminance and size, however, was reported to involve occipito-temporal regions. Numerical distance modulated activation in the bilateral anterior IPS and left precentral cortex. (For a review on Numerical Distance see below, Paragraph 2.1.3.)

A similar observation was made by Fias, Lammertyn, Caessens, and Orban (2007). Their study found the bilateral hIPS active for the comparison of numbers and letters, but not for luminance judgements. During comparison blocks, the participants had to decide which of two numbers was larger, which of two letters came later in the alphabet, or which of two squares was brighter. The absence of activity in the hIPS for luminance comparisons was interpreted to reflect the region's functional restriction to ordinal judgements.

Second, the responsiveness of the hIPS to numerical magnitude seems to be independent of notation.

In a PET study by Fias, Lammertyn, Reynvoet, Dupont, and Orban (2003) the left intraparietal sulcus was reported to respond not only to magnitude comparisons on digits, but also to comparisons on lines and angles. Furthermore, in an fMRI adaptation study by Piazza et al. (2007), the hIPS was found active for magnitude comparisons on Arabic digits and dot patterns, and it was also responsive to numerical distance. Piazza et al. (2007) report that the bilateral hIPS was activated by mental calculations with number words (e.g. 'Subtract five from eleven'), which were presented either visually or auditory, and compared to control sentences (e.g. 'The sailors threw the anchors into the bay').

The hIPS has recently been shown active for magnitude comparisons of dots and disk sizes, as well as for positive and negative integers (Chassy & Grodd, 2012). Their study located two peak activation sites in the right hIPS. A peak in the right hIP3 [MNI: 30, -51, 58] was found independent of notation, whereas activity in the right hIP2 [MNI: 45, -39, 45] was restricted to the magnitude processing of the analogue representations (disks and dots) and not found for the symbolic depiction, namely for positive or negative integers, suggesting the hIP3 as barycentre for numerical processing. By using different stimuli and imaging methods, these studies therefore provide converging evidence for the existence of a shared neural code for magnitude.

Third, the hIPS seems to be specified in the processing of numbers, when directly contrasted with objects or concepts from other categories, even if the task does not require the activation of numerical magnitude.

The hIPS was found active for the presentation of numbers, but not for letters and colour patches in a study by Eger et al. (2003). Participants were exposed to digits, letters and colours, both visually and auditory, and were instructed to respond only if the stimuli were identical across modalities (e.g. "2" and spoken "two", "B" and spoken "be"). Nine single Arabic digits, seven capital letters and seven colour fields were presented. Neural responses were determined for the incongruent presentations, in which no overt response was given. The hIPS was found active for the presentation of digits, independent of modality and therefore referred to as 'Supramodal Number Representation' System.

Taken together, these data suggest that the hIPS is a key region for numerical processing. However, clearly, it is not the only neural system involved.

Reportedly, the neural network for number processing also includes frontal areas, in particular in the inferior frontal (BA 44 and 45), dorsolateral prefrontal (DLPFC, BA 46 and 9) and superior frontal cortices (BA 6 and 8) (Chochon, Cohen, Van De Moortele, & Dehaene, 1999).

As previously mentioned, a meta-analysis of fMRI studies on arithmetic tasks by Arsalidou and Taylor (2011) showed left parietal activity for *addition* tasks, which was supplemented by left inferior and middle frontal activity (DLPFC, BA 9 and 46), as well as activity of the bilateral thalamus, right insula, right claustrum and bilateral cerebellum. For *subtraction* tasks, again, left parietal, but right inferior, middle and superior frontal activity (BA 9, 46, 10) was observed together with activation of the bilateral insulae. For multiplication tasks, parietal as well as inferior and middle frontal brain activity was dominant in the right hemisphere and supplemented by bilateral cingulate and thalamic activation. Activity in the left putamen was observed for all number tasks (Arsalidou & Taylor, 2011).

The findings are concordant with the triple code model by Dehaene and Cohen (1997), in which parietal activity is associated with mathematical performance in general; frontal activity is linked to strategic planning in mathematical thinking, and the putamen (part of the basal ganglia), together with the thalamus, are subsumed under the left cortico-subcortical loop, which is proposed to underlie visuo-verbal retrieval of mathematical facts (Arsalidou & Taylor, 2011; Dehaene & Cohen, 1997).

Based on this model, Arsalidou and Taylor (2011) suggest that prefrontal activity may reflect the short term memory (STM) demand during calculation tasks. More specifically, the inferior frontal gyri (BA 9) are interpreted to support simple numerical tasks (such as multiplication task, which are assumed to be mostly automatised), the middle frontal gyri (BA 46) are linked to tasks with an increased STM load and the superior frontal gyri (BA 10) are associated with multi-step problems (e.g. for combinations like $3 \times 5 + 6$). Also the cingulate gyri are suggested to support STM functions.

Left frontal and parietal activity was also observed in a short-term memory task by Attout, Fias, Salmon, and Majerus (2014). In their study, activity of the hIPS was elicited by numerical order judgements as well as short-term memory order judgements of letters. For the numerical order task, bilateral activity of the hIPS was observed, with a right hemispheric dominance. In the STM task, parietal activity was restricted to the left hemisphere, and supplemented by left inferior and superior frontal activity

(BA 6 and 48).

Finally, distinct patterns of activation of frontal, but also parietal cortices were found for adults and children during number processing. According to a meta-analysis by Kaufmann, Wood, Rubinsten, and Henik (2011), activation patterns in frontal brain regions were modulated by notation, but not by age: Inferior frontal (BA 45) and middle frontal (BA 46) activity was associated with non-symbolic presentation, and not found for numerical symbols in both, adults and children. The finding is interpreted to reflect higher working-memory and processing demands due to the visual complexity of non-symbolic representations (Kaufmann et al., 2011, p. 778). However, for the processing of non-symbolic presentation, in the intraparietal cortex, for adults and children, close, but not identical peaks of activation are found: whereas children are reported to activate bilateral anterior intraparietal regions, in adults, activity seems to be restricted to a right-lateralized and posterior intraparietal area.

The posterior parietal region corresponds to one of the three parietal circuits for number processing which are proposed by Dehaene et al. (2003). The authors assume that a distinct neural circuitry - namely a bilateral posterior superior parietal system - may support attentional, and in particular, visual and spatial orientation in the processing of number. Together with a language-related formation in the left Angular Gyrus (AG), both systems are proposed to supplement the bilateral hIPS, which is specified in the representation of quantity.

The assumption of an involvement of the posterior parietal sulcus in the processing of non-symbolic quantities was corroborated by findings from Santens and Gevers (2008) and Holloway, Price, and Ansari (2010). In the study by Santens and Gevers (2008), a standard fMRI evaluation was supplemented by a connectivity analysis. The authors report that numerical information, regardless of the input format (Arabic digits and dots), activated a portion of the left inferior parietal sulcus. However, activity in the posterior parietal sulcus was only found for the presentation of dots, suggesting separate pathways for the processing of symbolic and non-symbolic quantities. The posterior parietal sulcus is therefore proposed to provide an intermediate processing step for non-symbolic quantities, linking an early visual sensory analysis and a general, number-selective coding system, which does not exist for the processing of symbolic quantities (Santens & Gevers, 2008).

The notion was supported by Holloway et al. (2010). They compared judgements on the numerical magnitude of symbolic and non-symbolic stimuli. In the symbolic task, the larger of two Arabic digits, ranging from 1 to 9, was chosen. For the non-symbolic comparison, the larger of two amounts of white squares was detected. Confound variables were controlled. In both, symbolic and non-symbolic comparisons, the right inferior parietal lobe was active. Symbolic stimuli (contrasted with non-symbolic stimuli), elicited activity in the left Angular and superior temporal gyri, whereas non-symbolic (vs. symbolic) stimuli showed enhanced activity in the right posterior superior parietal lobe.

Consequently, the processing of symbolic and non-symbolic magnitudes is suggested to follow different pathways: symbolic quantities are assumed to directly address temporo-parietal regions; for the processing of non-symbolic quantities, on the other hand, a pathway via the posterior parietal sulcus may be involved in the mapping of external to internal representations (Dehaene et al., 2003; Holloway et al., 2010; Santens & Gevers, 2008).

Presumably, the processing of symbolic and non-symbolic magnitudes may also show lateral differences. For instance, Dehaene and Cohen (1997) have suggested that the processing of number symbols may be dominant in the left hemisphere because the left parietal lobe may provide a direct link to language-related brain regions. (The topic will further be discussed in Paragraph 2.1.4 on 'Number and Language'.)

The assumption that the bilateral inferior parietal cortices may host a central a-modal representation of quantity has recently been challenged by Friedrich and Friederici (2009). In their study, first-order hierarchical algebraic formulae ('mathematical syntax', e.g. $(a \cdot c < d + x) \vee (y + z > b)$ were compared to algebraic termini in a list (e.g. $y = z, w + w, u + b, b \cdot a$). The BOLD signal of the hierarchical compared to the flat structure was associated with the bilateral IPS, MFG, MTG and left IFG (Broca's area). Because both tasks only differed in terms of their structural complexity, but not in their numerical content, the authors suggest that the fronto-parietal brain system may reflect a heightened demand in visuo-spatial working memory. In a follow-up study, Friedrich and Friederici (2013) report that the activity of the bilateral IPS is still present, when hierarchical algebraic formulae such as $(a \cdot c < d + x) \vee (y + z > b)$ are compared to baseline or to structurally equivalent arithmetic expressions (e.g. $(7 \cdot 0 < 1) \wedge (3 \cdot 4 = 4 \cdot 3)$), even though the algebraic formulae did, again, not involve numbers.

The authors conclude: "Therefore, in order to reconcile the diverging and contradictory findings concerning the strict number sense and the IPS, we propose the consideration of (small) numbers as

elementary objects, which one might call 'number objects', and which represent a very simple form of structured information, made available for prefrontal regions." (Friedrich & Friederici, 2013, p. 8)

2.1.2 Subitizing

The quantity of up to four items can be perceived rapidly, accurately and confidently without counting. This ability is referred to as 'subitization' or 'subitizing', derived from Latin *subitus* ('sudden') (e.g. Dehaene, 2011; Cutini, Scatturin, Basso Moro, & Zorzi, 2014; Ester, Drew, Klee, Vogel, & Awh, 2012; Piazza, Mechelli, Butterworth, & Price, 2002; Piazza, Mechelli, Price, & Butterworth, 2006; Revkin, Piazza, Izard, Cohen, & Dehaene, 2008; Vuokko, Niemivirta, & Helenius, 2013).

Apparently, fewer than four items are perceived within 40 - 100 ms/item, but more than four items have to be counted, which results in increased reaction times of up to 250 - 350 ms/item, whereas accuracy rates rapidly drop (Trick & Pylyshyn, 1994).

The discontinuity of the processing, starting from the fourth or fifth item has led to the assumption that small numbers and large numbers are processed differently. Consequently, subitizing was suggested to be represented by a first core system for small and exact numerosities, which may be distinguished from a second core system for large, but approximate magnitudes (Feigenson et al., 2004).

Apparently, both, subitizing and counting, are reflected by activity in the parietal cortices (Cutini et al., 2014; Piazza et al., 2002), but the hemodynamic response for counting seems to be stronger (Cutini et al., 2014; Piazza et al., 2002) and it seems to peak later than the response for subitizing (Cutini et al., 2014; Vuokko et al., 2013).

In their PET study, Piazza et al. (2002) presented sets of dots ranging from 1-4 and 5-9. The dots were distributed either randomly or canonically. Piazza et al. (2002) found increased left-lateralized parietal activation for counting, which was not involved in subitizing. For the counting > subitizing contrast, right superior parietal areas, left inferior/middle parietal areas and the right anterior insula were active. However, no distinct brain regions were identified for subitizing, which was explained by the increased demand of the counting procedure on visuo-spatial attention and working memory processes.

Cutini et al. (2014) used functional Near-Infrared Spectroscopy (fNIRS) to investigate the modulation of the hemodynamic activity in parieto-occipital regions during subitizing (2-3 dots) and counting ('estimation' of 5-6 dots). Two to six dots were presented in three different sizes and the participant had to give an oral response of their quantity. After each set, a response to a corresponding Arabic digit (digits 2-6) was requested, which served as control condition.

During dot quantification, the right posterior parietal cortex (PPC) and the bilateral intraparietal sulci (IPS) were sensitive to numerical magnitude. Especially the right IPS is reported to show a striking magnitude-dependent response, with a low hemodynamic activity for 2 and 3 dots, but a sudden increase for 5 dots and a plateau (i.e. a sigmoid fit). In the subitizing range (2-4 dots) the hemodynamic response was significantly earlier than in the counting range (5-6 dots).

Cutini et al. (2014) interpret their findings as evidence for the assumption that subitizing is part of the *Object Tracking System* and distinguishable from the *Approximate Number System* for bigger sets of items (Ansari, Lyons, van Eimeren, & Xu, 2007).

The findings were complemented by a MEG study by Vuokko et al. (2013). In their study, brain activity of subitizing and counting differed both spatially and temporally. Two to eight randomly located black dots were silently enumerated by the participants, and quantification was indicated by pressing a button. For subitizing, 250 ms after stimulus presentation, activity peaked in the bilateral temporo-parietal lobes were observed. For counting, two brain activity peaks 400 - 900 ms after stimulus presentation were observed: first, after 500 - 600 ms, channels above the vertex, temporal and parietal areas showed activation, while bilateral frontal activity showed a linear increase in activation in the entire time window.

According to Vuokko et al. (2013), the right temporo-parietal junction may serve as neural substrate for visual attentional engagement, which might host a link between subitization and object recognition.

The findings indicate that both subitizing and counting are reflected by bilateral parietal activity, with an increased signal strength for counting and different temporal patterns for counting and subitizing. For counting, additional frontal activity may be assumed. The rapidness of subitizing is interpreted to resemble the time course of object recognition, and is therefore linked to the Object Tracking System, which governs the individuation of objects and the allocation of attention over several items (Piazza, Fumarola, Chinello, & Melcher, 2011; Vuokko et al., 2013)

2.1.3 Mental Number Line and Numerical Distance

As mentioned at the beginning of the chapter (see Section 2.1), in number comparison tasks typically a distance effect is observed (Moyer & Landauer, 1967). The finding can be explained with a spatial representation of numerical magnitudes, which is also referred to as *mental number line* (Moyer & Landauer, 1967; Dehaene et al., 1993; Dehaene, 1996, 2011; Pinel et al., 2004; Piazza et al., 2007).

The numerical distance effect as been replicated behaviourally in a large number of comparison tasks for miscellaneous properties, such as weight, length, physical size and luminance (Pinel, Dehaene, Riviere, & LeBihan, 2001; Pinel et al., 2004; Cohen Kadosh et al., 2005; Zhou et al., 2006; Soltész, Szűcs, Dékány, Márkus, & Csépe, 2007). The effect seems independent of number format, such as for the presentation of Arabic digits (Bulthé, De Smedt, & Op De Beeck, 2014; Moyer & Landauer, 1967; Pinel et al., 2001; Szűcs & Csépe, 2004; Van Opstal & Verguts, 2011), number words (Dehaene, 1996; Pinel et al., 2001; Szűcs & Csépe, 2004) and dot patterns (Bulthé et al., 2014; Koechlin, Naccache, Block, & Dehaene, 1999) and independent of presentation mode, e.g. visual and auditory (Szűcs & Csépe, 2004).

Again, numerous functional imaging studies suggest that the bilateral hIPS might be responsive to numerical distance (Piazza & Dehaene, 2008; Pinel et al., 2004; Piazza et al., 2007).

In the aforementioned fMRI adaptation study by Piazza et al. (2007), large portions of the bilateral IPS showed distance-dependent recovery from adaptation for the far compared to close deviants, with a subtle left-hemispheric dominance for digits compared to dots. In addition, activation of the bilateral prefrontal and inferior frontal cortices was observed for numerical distance. In their study, subjects were adapted to the values 17, 18, and 19 or 47, 48 and 49, which were presented as digits or dot patterns. Afterwards either the deviant number 20 or 50 was shown to them. For the first group of numbers, the number 20 served as 'close deviant' and for the second group as 'far deviant'; conversely for number 50.

Pinel et al. (2004) have reported that the bilateral hIPS is not only responsive to numerical distance, but also to size distance. Numerical distance was also reflected by activity in the left precentral gyrus. Their study compared either the magnitude, physical size or luminance of Arabic digits. Size comparisons were also performed with letters. The distance effect was quantified by comparing close to far deviants. However, distance effects along a given dimension affected reaction times and brain activation only when subjects attended to that dimension.

Cohen Kadosh et al. (2005) derived a similar finding for numerical, luminance and size judgements. Here, the left IPS, along with the right superior and middle temporal lobe, showed a task-specific BOLD response for numerical distance.

Cutini, Scarpa, Scatturin, Dell'Acqua, and Zorzi (2012) did not only investigate numerical distance but also the SNARC effect with fNIRS. The 'Spatial-Numerical Association of Response Codes' provides a link between numbers and space: in magnitude comparisons, responses for large numbers are faster with the right hand than with the left hand, whereas the converse is found for small numbers. In their study, the magnitude of a single Arabic digit was compared to the reference number five (which was not presented). In SNARC compatible trials, the response 'larger' was made with the right index finger on the right button, in SNARC incompatible trials it was made with the left finger on the left button. Again, a hemodynamic signature of numerical distance (close vs. far) and of SNARC (incompatible vs. compatible) was detected in the bilateral hIPS, and an additional neural correlate for SNARC was observed in the left Angular Gyrus or temporo-parietal junction. However, reportedly, the effect was only found with HbO (oxygenated hemoglobin) and not with HbR (desoxygenated hemoglobin). fMRI represents HbR concentrations and is assumed to be weaker than HbO (Cutini et al., 2012).

Indeed, in a recent multi-voxel pattern analysis on fMRI data by Bulthé et al. (2014), a neural response for distance was not found for Arabic digits, but only for dot patterns. Again, participants were instructed to judge whether a given number was larger or smaller than five. The numbers were either presented as digits or dots. Pattern classification decoded a neural distance effect in parietal, frontal and the temporal cortex for dot patterns, but for symbolic digits no magnitude related activity was captured. Because no common neural patterns for non-symbolic and symbolic magnitudes were found, Bulthé et al. (2014) suggest that both formats do not have a representational overlap.

The findings are in line with the results from a multivariate pattern recognition analysis on functional MR data by Eger et al. (2009). Distinct parietal patterns were recognized for dots and digits, albeit the recognition of the digits was less accurate. Numerical distance activation patterns were only detected for small and close non-symbolic dot patterns. According to the authors, neither Arabic digits, nor quantities separated by a large ratio showed an effect, suggesting that they were encoded by distinct neuronal substrates.

To sum up, the **numerical distance effect** is reported to manifest in parietal areas, in particular

in the inferior and superior parietal lobe (Bulthé et al., 2014; Cohen Kadosh et al., 2005; Kaufmann et al., 2005; Piazza et al., 2007; Pinel et al., 2001, 2004). In addition, responsiveness to numerical distance was observed in the bilateral anterior Insula (Kaufmann et al., 2005; Piazza et al., 2007), the inferior and superior frontal gyrus (Bulthé et al., 2014; Pinel et al., 2004; Piazza et al., 2007) and the anterior and posterior cingulate gyrus (Kaufmann et al., 2005; Pinel et al., 2001).

It must be noted, though, that the numerical distance effect seems to be robust for non-symbolic magnitudes, but the results for symbolic representations, namely for digits, are inconsistent (Bulthé et al., 2014; Eger et al., 2009).

It is currently under debate, whether number words and number symbols automatically activate magnitude representations or not (Cohen Kadosh & Walsh, 2009; Lindemann, Rueschemeyer, & Bekkering, 2009). According to Lindemann et al. (2009) number words and unfamiliar number symbols are coded superficially, and they do not automatically activate magnitude information. They claim "under conditions of automatic processing, complex and unfamiliar number symbols will be merely transcoded and represented asemantically in a perceptual, linguistic, or phonological format" (Lindemann et al., 2009, p. 341). This would explain the absence of a distance effect for number symbols.

Beyond that, neural correlates of the numerical distance were not resulting from parametric modulation, instead, either small distances were compared to the large distances, or far to close deviants (Cutini et al., 2012; Fulbright, Manson, Skudlarski, Lacadie, & Gore, 2003; Cohen Kadosh et al., 2005; Kaufmann et al., 2005; Piazza et al., 2007; Pinel et al., 2001, 2004), in one study, the distances were divided into three groups (Bulthé et al., 2014).

2.1.4 Numbers and Language

According to Spelke (2003), adult human beings as well as non-primate animals and pre-verbal infants are assumed to be provided with a number core system, which is independent of language. Furthermore, Spelke and Tsivkin (2001) and Feigenson et al. (2004) have suggested that the number core system may further be subdivided into a 'core system 1' for small, exact numbers and a 'core system 2', which provides knowledge about large, approximate numerosities.

Feigenson et al. (2004) suggest that both initial core systems are independent from language, but limited in their representational power. They do not support abstract mathematical concepts, such as exact integers, not to mention fractions, square roots and negative numbers. Natural language is assumed to provide us with the ability to combine the two distinct systems, which may finally result in the uniquely human capability to acquire formal mathematics.

The authors conclude that mathematics are 'easy' and transparent, as long as they are solely based in one of the core systems, but as soon as numerical thinking goes beyond the capabilities of the core system, it becomes 'hard'. Formal mathematics, for instance, goes beyond the intuitive sense of numerosity as provided by the core systems.

> The new, hybrid system captures the benefits of both, initial, language-independent systems and overcomes the specific limits of each system. Like the exact small number system, it is discrete, exact, and applies to persisting individuals; like the approximate large number system, it serves to represent sets with no upper bound and with explicit cardinal values. Because language serves to link the two types of representations that compose this system, however, representations within the system depend on it (Spelke & Tsivkin, 2001, p. 83).

According to Condry and Spelke (2008), the development of composition can also be observed during the numerical language acquisition of 3-year-old children. Even though the children may be able to correctly count to 'ten', at the beginning, their ability to comprehend and correctly assign number words to objects is limited to the number words 'one' and 'two', where 'one' refers to *one individual*, and 'two' and all the other number words refer to 'some' or *more than one* individual. The finding is interpreted to reflect the fact that two distinct numerical representation for small and exact or large and approximate numerosities are accessed, but due to limited language capabilities, they cannot be combined (Spelke & Tsivkin, 2001; Condry & Spelke, 2008).

Because both numerical core systems are not dependent on language, they refer to various sensory modalities and they can be applied to different stimuli and tasks, according to Wiefel, Pauen, and Dueck (2009) they are *abstract*.

Presumably, the bilateral hIPS may provide the cerebral foundation for an abstract and non-verbal numerical core system, which may be distinguished from a verbal faculty, which is assumed to rely on the left Angular gyrus (Dehaene et al., 2003).

According to Dehaene et al. (2003) and Feigenson et al. (2004), in particular the system for representing large and approximate numerical magnitudes has become well characterized with the bilateral hIPS. But as mentioned before in Chapter 2.1.2 'Subitzing', parietal areas are also consistently found active for the enumeration of small and exact quantities.

However, although both hemispheres of the parietal lobe are proposed to manipulate quantity information, only the left parietal lobe is assumed to provide a direct connection of the magnitude representation with the verbal code (Dehaene & Cohen, 1997).

The lateralization of the parietal lobes is still under debate. There is evidence that small and precise quantification may predominantly activate the left parietal lobe, whereas activity for the processing of large and approximate numerosities may be assigned to the right IPS and may presumably also comprise right frontal areas (Dehaene & Cohen, 1997; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza et al., 2006, 2007).

In particular, analogue number notations (such as dot patterns and disk sizes) are associated with the processing of imprecise magnitudes and assigned to the right hemisphere, whereas symbolic magnitudes (digits, number words) are interpreted to elicit precise magnitude representations, which are processed in the left hemisphere (Arsalidou & Taylor, 2011; Chassy & Grodd, 2012; E. Klein et al., 2014)

The fMRI results from Piazza et al. (2007), for instance, have shown a distance-dependent adaptation for dots and Arabic digits, which was present in both hemispheres of the parietal cortices, but an asymmetry across notations was found in the left hemisphere only, suggesting that only the left parietal lobe has been affected by (precise) number symbols, while the right parietal lobe is assumed to keep approximate representations for both, digits and dots.

The responsiveness of the left parietal lobe to precise numerical judgements was also reported by Piazza et al. (2004). The authors conclude that the BOLD signal in the right IPS may be correlated with approximate judgements, whereas the left IPS might be responsive to exact judgements (Piazza et al., 2006).

A similar asymmetry was concluded by Chassy and Grodd (2012). They found that analogue stimuli (disks and dots) are processed in the right hemisphere, whereas the processing of symbolic stimuli is reported to encompass right and left hemispheric regions.

And also Holloway et al. (2010) as well as Santens and Gevers (2008) report lateral differences in the processing of symbolic and non-symbolic magnitudes: Reportedly, left (parietal) Angular and superior temporal gyri were more active for symbolic stimuli (Holloway et al., 2010), whereas the right posterior superior parietal lobe was more active for non-symbolic stimuli (Holloway et al., 2010; Santens & Gevers, 2008), and supplemented by a large area in the visual cortex, which is interpreted to reflect a greater visual demand in the non-symbolic condition (Holloway et al., 2010; Santens & Gevers, 2008).

And Holloway et al. (2010) have reported a right hemispheric dominance for both, digits and squares, but Santens and Gevers (2008) found that the processing of digits and dots is restricted to the left hemisphere, which might possibly be explained with a higher precision required for the enumeration of dot patterns, compared to squares.

And the left-bilateral-right pattern in the parietal lobe for addition-subtraction-multiplication (cf. p. 13), which was observed by Arsalidou and Taylor (2011), supports the notion that left parietal areas are involved in the processing of exact judgements (addition, subtraction), whereas right parietal regions may contribute to continuous numerical tasks (multiplication).

However, both Bulthé et al. (2014) and Eger et al. (2009), have reported bilateral activity in the IPS (and various other regions) for dot patterns, but an absence of inferior parietal activity for symbolic magnitudes.

Bulthé et al. (2014) claims that symbols and non-symbolic representations are decoded in different brain regions: whereas for dots, in both hemispheres a high decoding accuracy in wide frontal, parietal and temporal regions was achieved, a significant decoding accuracy for symbols was only observed in the left SPL, inferior occipital cortex, fusiform gyrus and right superior frontal gyrus (Bulthé et al., 2014, p. 317). The authors report that they did not find any overlapping neural regions for symbolic and non-symbolic magnitudes, and therefore suggest that both formats do not share a representational overlap.

There is strong evidence to suggest that the bilateral horizontal segments of the intraparietal sulci play a key role in the processing of numerical magnitude. Their activity seems to be independent of notation, they are involved in numerical comparisons, and responsive to numbers even when the numerical

magnitude is not necessary to solve the task. The left hIPS may serve as an interface to language related brain regions. Presumably, activity in inferior, dorsolateral and inferior frontal areas may provide short term memory functions (Arsalidou & Taylor, 2011). Furthermore, posterior superior parietal areas may be involved in the attentional, visual and spatial processing of numbers (Dehaene et al., 2003). Superior parietal areas also seem to be involved in the spatial processing of objects (e.g. Zachariou et al., 2015).

2.2 Objects

For many reasons, object perception is extremely difficult: The most fundamental problems are, first, that objects may vary in their position, scale, pose, luminance, and colour, and they may even be deformable in shape, which is sometimes called the 'invariance problem'. Furthermore, the object may be part of a cluttered scene or partly hidden, but we are still able to assign its features to the correct object, resulting in a unified concept. This is referred to as the 'binding problem'. How do we manage to perceive coherent, unified objects? How do we extract them from an unlimited set of images on the retina? The neural mechanisms underlying the humans' ability to solve such a complex task with exceptional ease and speed, is one of the central questions in cognitive neuroscience.

According to Spelke (2003), human beings, as well as non-human animals, are provided with a core system of *object representation* which is specified in the identification of object boundaries. The perception of objects is assumed to rely on their cohesion, on the continuity of their movement and the fact that the interaction of objects is dependent on their spatial proximity.

To perceive an object, we have to link its features to a coherent whole. *Object recognition*, on the other hand, goes beyond the scope of *object perception*. In human adults, the product of perception may be transferred to object *recognition*, which is closely linked with memory (Gazzaniga, Ivry, & Mangun, 2002, p. 193 ff.) and language.

Object recognition is defined by the ability to assign labels to a particular object or picture of an object (e.g. a noun). Objects may be identified with a precise label (e.g. 'chair'), or categorized with coarse labels (e.g. 'furniture') (DiCarlo, Zoccolan, & Rust, 2012; DiCarlo & Cox, 2007). Hence, object recognition refers to our ability to comprehend the meaning of an object.

Early neuroscientific research on lesion studies from patients suffering from different forms of visual agnosia have led to the notion that perception and recognition rely on different processes. A brain lesion may, for instance, result in an 'apperceptive visual agnosia'. Ferreira, Ceccaldi, Giusiano, and Poncet (1998) reported a case study from a patient with a lesion in the bilateral occipito-temporal lobes, who was suffering from apperceptive agnosia. He was still able to analyse shapes, colours and motions, but he was not able to perceive an object. The authors state that "[d]espite the fact that he could describe a visually perceived object in detail, he failed to relate individual elements to the whole, and consequently, he was not able to identify it" (Ferreira et al., 1998, p. 382).

A similar, but smaller, occipito-temporal lesion was reported to result in 'associative visual agnosia' by Jankowiak, Kinsbourne, Shalev, and Bachman (1992). In this case, the patient was still able to perceive the form and function of an object, and he was even able to categorize objects, but he was not able to identify it. However, if he was allowed to use auditory or tactile sensations, his performance was excellent, he could thus identify objects, if he was allowed to touch them, and also with the help of auditory perception, like 'jingling keys'. The authors have concluded that the patient could derive an internal visual images from semantic memory, but he was not able to match the object with the internal image (Jankowiak et al., 1992).

2.2.1 Neural Core Systems of Object Perception

The findings from studies on lesions in humans and monkeys were integrated into an influential dual path model by Mishkin, Ungerleider, and Macko (1983). In their model, the processing of visual perception and recognition relies on a *ventral*, or occipito-temporal pathway, comprising striate, prestriate and inferior temporal areas. The ventral pathway thus became popular under the name 'what'-pathway. It was distinguished from the *dorsal*, occipito-parietal pathway for spatial perception, and is referred to as 'where'-pathway.

Nowadays, new methods in cognitive sciences, such as non-invasive functional imaging and ERP studies, which can be applied on healthy subjects, as well as experiments on monkeys, have achieved to identify a number of distinct visual areas along the ventral visual stream.

Studies on rhesus monkeys have led to the assumption that the ventral visual stream processes a progressive series of 'visual re-representations'. The process is starting from the visual image striking the eye, i.e. from retinal ganglion cells, the visual information is conveyed via the lateral genital nucleus (LGN) to the lower visual cortex V1 to the cortices V3 to V4, terminating in the inferior temporal cortex (DiCarlo & Cox, 2007).

According to Gazzaniga et al. (2002), 90% of the fibers from the optic nerve terminate in the LGN. The LGN is located in the most lateral, inferior region of the thalamus, and consists of six layers. All layers receive input from the optic nerve and send output to the visual cortex, but half of the layers receive input from the ipsilateral retina, the other half from the contralateral eye.

The first cortex, which is carrying visual information, is the V1, a posterior and medial portion of the occipital lobe, and also referred to as *primary visual cortex* or 'striate cortex' (BA 17). The V1 consists of several layers, which are partly organized in columns. Many neurons in the V1 were found to be selective to orientation and to direction. In addition, binocular receptive fields were found. Furthermore, it is assumed that the V1 might comprise blob cells, which are sensitive to wavelength. Visual information is processed in parallel (Bear, Connors, & Paradiso, 2007; Gazzaniga et al., 2002).

For the visual cortices V1, V2 and V4, complete retinotopic maps have been discovered, and even the posterior inferior temporal (IT) cortex seems to host coarse retinotopy (De Beeck, Torfs, & Wagemans, 2008; DiCarlo et al., 2012).

Results from ERP studies by Di Russo, Martínez, Sereno, Pitzalis, and Hillyard (2002); Schendan and Lucia (2010) have led to the conclusion that initial, bottom-up object perception in the primary visual area (striate cortex, BA 17) is found as early as 55 to 95 ms after an object is displayed (early P100). After 100-140ms (late P100), activity is spreading to ventral occipito-temporal cortices (Di Russo et al., 2002; Schendan & Lucia, 2010).

The primary visual cortex has simple cells which preferentially respond to oriented bars. It is assumed that the receptive field size and the preferred complexity of object features increases along the ventral stream (Riesenhuber & Poggio, 2002)

Actually, on top of the ventral stream, individual neurons in the inferior temporal (IT) cortex in monkeys seem to be responsive to *classes* of objects, such as faces or other complex shapes (DiCarlo & Cox, 2007; Riesenhuber & Poggio, 2002). Furthermore, these cells were found to be robust to object transformations such as changes in scale and position (Riesenhuber & Poggio, 2002).

Human fMRI data have shown a similar robustness to invariance in a region which is referred to as lateral occipital complex (LOC). The LOC is considered to be a homologue to the inferior temporal cortex in monkeys. Arguably, the LOC plays a key role in human object recognition (Riesenhuber & Poggio, 2002).

The LOC is located in the fusiform gyrus, extending dorsally and ventrally. In a fMRI study by Malach et al. (1995), the region was not only found active for images of famous faces and common objects (e.g. tools) but also for images of unfamiliar 3D objects, namely of Henry Moore sculptures, which were compared to scrambled phase textures.

In a recent fMRI and MVPA investigation, Erez, Cusack, Kendall, and Barense (2015) confirmed the involvement of the LOC in the 'conjunctive coding of complex object features'. According to them, the LOC is supplemented by activity in the perirhinal cortex (PRC), a structure within the medial temporal lobe, which is traditionally assumed to be involved in long-term memory functions. Recently, the PRC has been proposed to constitute the apex of the ventral stream. In the study, a cone-shaped figure was applied with three novel features. The features A, B and C were either applied as a single feature (e.g. 'A') or combined (e.g. 'BC'). The resulting objects were presented one after another, and from different viewpoints. Participants had to perform a 1-back memory task, which means that they had to press a button when they saw the object twice in succession, independent of its viewpoint. The approach allowed to investigate whether there was a specific representation of the feature conjunction comprising an object which was unlike its component parts. The idea was that if the object combinations comprising of all features were equivalent (A+BC = B+AC = C+AB), the result would speak to the notion that the combinations were not coded by specific patterns of activity, and therefore consistent with non-local binding. According to the non-local binding mechanism, features are represented by different neural structures, and bound by their co-activation. If the patterns were not equivalent, the neural code was expected to be conjunctive ('explicit conjunctive coding'). Explicit conjunctions were found to be coded along the ventral visual stream, comprising V4 and LOC, extending anteriorly to the perirhinal cortex (PRC), independent of their viewpoint (Erez et al., 2015). The results suggest that feature binding is the consequence of explicit conjunctive coding along the visual ventral stream (VSS).

We've seen that visual information seems to follow a distinct route. The process starts from the

retinal ganglion cells in the eye and seems to be transferred via the LGN to the primary visual cortex (V1). The information now appears to follow the ventral visual stream (VVS) along the V1, V3 and V4 and it finally terminates in the temporal cortex (DiCarlo & Cox, 2007). Posterior regions of the VVS are proposed to process low-level features and more anterior regions of the VSS are processing increasingly complex conjunctions of these simpler features (Erez et al., 2015).

2.2.2 Spatial Attention

It is now general consensus that object perception is mediated by various cortical regions along the ventral stream. But how do spatial processing mechanisms – which are attributed to be processed along a dorsal visual processing stream, comprising the parietal lobes – contribute to feature binding?

According to the *feature integration theory of attention* (FIT) by Treisman (1998), spatial attention plays a central role in object perception. According to the FIT, humans are provided with two 'maps', which are accessed in parallel: First, a location map, which is dependent on attention, in which we locate a region. In a separate feature map, we are provided with the ability to correlate whether a specific feature, for example, the colour 'red', is present in a certain object. For the application of the feature map, attention is not required. In some cases, the sole output of a feature map may be sufficient, it may, for instance, provide us with the information that we have perceived something 'red', but we cannot tell from the feature map, where the red object was or whether the object comprised other features such as 'motion' or 'shape'. To solve the binding problem, and to put 'what' and 'where' together, we have to move the attention window within the location map and at the same time, we synchronize whether the features in the attended region match with the features from the feature map. Evidence for the theory comes from behavioural experiments, in which so called 'illusory conjunctions' were investigated. In such an experiment, the visual attention is manipulated by influencing the fixation and the amount of time in which the object may be allocated. After a brief exposure to, for example, a red circle next to a green triangle, participants sometimes report that they have seen a red triangle or a green circle, namely an 'illusory conjunction'.

Various visual search paradigms have been used to study visual attention. In such a task, subjects are typically informed about the distinctive features of a target that they have to look for. The target is displayed among a number of distractors, and the subject has to report its presence. Early visual search tasks by Treisman and Gelade (1980) have shown that it is very easy to detect a target if it is defined by a single distinctive feature (e.g. a red triangle among green triangles), but in case the target is defined by more features (e.g. a red triangle among green triangles and red squares), the search becomes difficult and inefficient.

The findings are interpreted to indicate that we are provided with an early, preattentive, feature registration ability, which allows us to segregate textures and to perform figure-ground grouping. Conjunctions - which are comprising more than one feature - on the other hand, require focal attention.

The specific contributions of cortical regions along the ventral as opposed to the dorsal stream were subject of a recent functional imaging study by Zachariou et al. (2015). In their (first) experiment, images of two identical, complex everyday objects (e.g. chairs, axes, tables, pipes) were presented. The objects were identical, but they could either differ in their overall texture ('texture-type difference') or the texture of different parts of the objects were varied ('texture-location difference'). For instance, in the 'texture-location difference' condition, two identical armchairs were presented, but the backrest of the chair had texture A and the seat area had texture B, and vice versa for the second armchair. Participants performed a same-difference task with a button press.

In response to texture-type as well as texture-location differences, significant activity was observed along the Ventral Visual Stream.

But for the texture-location > texture-difference contrast, significant BOLD differences in the parietal lobe (bilateral precuneus, superior parietal lobe, right inferior parietal lobe, BA 7,40,19), but also in the left middle temporal gyrus and left inferior temporal gyrus (BA 37) were observed. The converse texture-difference > texture-location contrast did not yield significant results. (Zachariou et al., 2015)

The parietal lobes are also involved in the spatial location processing of faces as opposed to a working memory tasks of faces (Courtney, Ungerleider, Keil, & Haxby, 1996). In their PET study, in a randomly distributed matrix of black squares, pictures of faces appeared. The subject had to remember either three faces or the three locations of the faces. The tasks were contrasted against a sensorimotor control task, in which scrambled faces were presented and were also followed by a button press by the subject. Both, the face as well as the location detection task, elicited right occipital-fusiform activity (BA 19). Whereas the

location memory task involved bilateral superior parietal activity (BA 7), the face memory task elicited bilateral fusiform (BA 19), right middle frontal, bilateral inferior frontal and cingulate activity.

The results lead to the assumption that the parietal lobes play a central role in the processing of spatial attentional control in object perception.

The occipital lobes also seem to be involved in the processing of spatial attention. Silver, Ress, and Heeger (2007) argue that the areas V1, V2 and V3 are not only activated by direct visual stimulation, but also during the maintenance of attention, which is required to perform a visual detection task. In their fMRI study, participants had to watch out for a plaid annulus, which was presented in a delayed period of 2 to 16 seconds. Silver et al. (2007) report enhanced activity in V1, V2 and V3, which was observed during the 'maintenance period' for the attended region, compared to ROIs corresponding to peripheral, unattended portions of V1, V2, and V3.

Earlier, spatial information was suggest to follow a dorsal pathway and to encompass parietal areas (Mishkin et al., 1983), indeed, also recent findings suggest that occipital areas may support spatial attention (Silver et al., 2007), whereas parietal regions seem to mediate the mapping of special features of an object to its particular locations (Zachariou et al., 2015).

2.2.3 Object recognition and Language

Object recognition, as opposed to object perception, is defined by our ability to apprehend the meaning of an object. It thus refers to the capability to correctly identify, categorize and label an object and to match objects to one another.

Object recognition is presumed to involve middle temporal areas, namely the anterior fusiform gyrus (also referred to as *lateral occipital complex*; LOC) (Bar et al., 2001; Schendan & Lucia, 2010), and frontal areas (Schendan & Lucia, 2010). The left ventral and anterior temporal cortex as well as bilateral prefrontal cortices may also support a fine-grained semantic analysis (Clarke, Taylor, Devereux, Randall, & Tyler, 2012). The bilateral fusiform gyrus together with the occipitotemporal sulcus (OTS) are suggested to be involved in explicit object identifications (Bar et al., 2001). In their fMRI study, images of objects were presented repeatedly, but only briefly (26ms) and in addition, they were masked. Consequently, the image could not be identified immediately, but performance increased[1]. The subjects were instructed to rate whether they had identified the presented object on a 1-4 scale. The fMRI signal in the anterior fusiform gyrus, as well as in the ventral-temporal OTS, was linearly related to object recognition, whereas the same analysis in V1, V2, and V4v yielded a flat line.

Activity in the bilateral parahippocampal gyri, on the other hand, was only present in the non-masked condition, when recognition was easy and not interrupted, which is interpreted to indicate its involvement in post-recognition mechanisms, for instance, the activation of semantic knowledge and memory consolidation (Bar et al., 2001).

Hence, extracting a more detailed, exact identification of an object, is assumed to require an additional fine-grained analysis which is supported by anterior temporal regions.

Investigations regarding the neuronal time course of object perception and object recognition suggest that occipito-temporal regions for initial, bottom-up object perception may interact with frontal and temporal brain areas which support object recognition (Clarke et al., 2012; Schendan & Lucia, 2010).

According to Schendan and Lucia (2010), object recognition or 'object model selection' is defined by our ability to select the best match to the percept from memory.

In their 'two-state interactive account' object perception or *object-sensitive activity* is assumed to reflect feature-detection, structural encoding and perceptual categorization, for example, the detection of an object within a scene, and the second, *object model selection* phase, is supposed to activate visual object knowledge and thus involves higher-order cognitive functions, which enables us to make categoric decisions (Schendan & Lucia, 2010).

In the ERP study by Schendan and Lucia (2010), the perception and recognition of intact and scrambled grey-scale photographs were investigated. Results suggest that 'first state', i.e. initial, bottom-up object-sensitive activity, rises in the occipito-temporal cortex as early as 95 to 200 ms after an object is displayed. The activity in the lateral occipital sulcus (LOS) is reported to be followed by a second peak after 120-140 ms (late P100), spreading to the posterior fusiform gyrus. Together with an occipito-temporal negativity (N170), a centro-frontal 'vertex positive peak' was found to rise after 145-195 ms.

[1] Actually, subjective identification ratings are reported to increase for the second and to peak for the third presentation, but to drop with the fourth and fifth repetition.

After 200 ms, the 'second state', i.e. *object model selection* takes place, in which the percept is assumed to be matched to memory. The so-called fronto-central N3 complex, starting with a fronto-polar positivity (P250), extending to occipital, inferior temporal and fusiform areas is assumed to support the selection of object categories (Schendan & Lucia, 2010).

Clarke et al. (2012) held an MEG study investigating the time course of perceptual and semantic effects associated with the processing of complex and meaningful visual objects. Colourful images were presented to the subjects, and additional non-meaningful pictures of sculptures were presented as filler items. The subjects were instructed to name the meaningful pictures (e.g.'tiger') or to respond with the word 'object'. The number of the objects' shared features (e.g. 'has eyes') and distinctive features (e.g. 'has a hump') was calculated. Early semantic effects are related to shared semantic features. In line with previous results (Di Russo et al., 2002; Schendan & Lucia, 2010), initial object perception was reflected by activity in the bilateral occipital cortex, starting 75 ms after the picture was presented. Rapid semantic effects along the left ventral temporal cortex to the anterior temporal lobe were observed between 84 and 120ms. Because the activity was higher for shared features compared to distinctive features, activity was interpreted to "support coarse-grained or categorical dissociations but not a more differentiated representation of the object" (Clarke et al., 2012, p. 193). Shared, or overlapping, features are thus assumed to support object categorization. After 200 ms, for both, shared and distinctive features, overlapping activity along the ventral temporal cortex becomes apparent, with greater responses for concepts with distinct features in the ventral and anterior temporal cortex as well as bilateral prefrontal cortices. Effects of relative distinctiveness are reported to be lateralized to the left ventral stream (Clarke et al., 2012). Clarke et al. (2012, p. 195) argue that initial coarse representations, which are based on shared semantic information, bear on feed-forward processing, whereas the integration of the concept's distinct features, reflecting the fine-grained semantic analysis, results from recurrent activity in the anterior and posterior temporal lobes.

Hence, over time, perceptual and semantic information is extracted from visual objects, that together enable meaningful visual object recognition, which is essential to categorize and finally, label and name an object (Clarke et al., 2012).

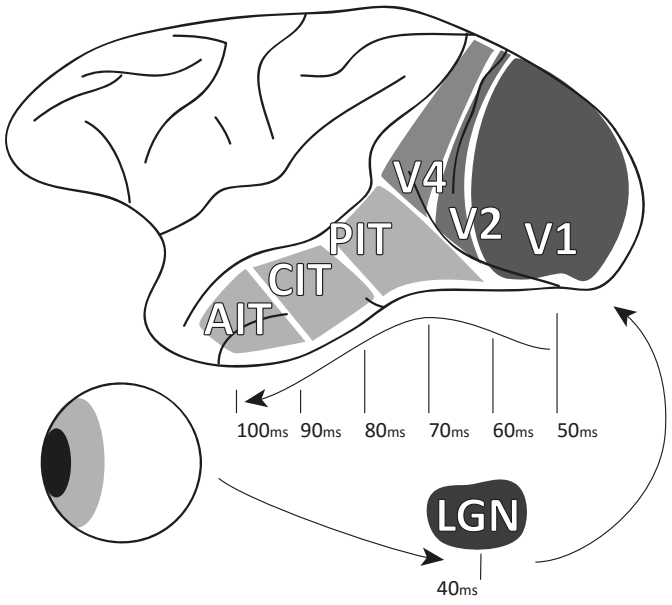


Figure 2.1: Neural time course of object recognition. Illustrated on a monkey brain. Adapted from DiCarlo et al. (2012, p. 419). PIT = posterior, CIT= central, and AIT = anterior inferior temporal cortex

Grill-Spector, Kourtzi, and Kanwisher (2001) and DiCarlo et al. (2012) state that the lateral occipital cortex (LOC) is consistently found active when human subjects view pictures of objects. They conclude that the inferior temporal region – comprising the fusiform gyrus – may not only be necessary but, presumably, even sufficient for object recognition.

Furthermore, in line with previous findings, an anterior-posterior gradient in the temporal lobe is supposed to contribute to object representations, with anterior structures contributing more to the representation of complex conceptual associations (Peelen & Caramazza, 2012).

In the fMRI study by Peelen and Caramazza (2012), pictures of everyday objects were presented to the participant. Half of the objects were typically found in a kitchen (e.g. corkscrew, garlic press), the other half was usually kept in a garage or workplace (e.g. screwdriver, pliers); in addition, half of the objects was manipulated by a rotation movement, and the other half by a squeeze movement. In two different runs the participants were asked to match two of the objects either according to the location or the action associated with the objects by pressing a button. Information about actions and locations were processed in more anterior regions of the temporal lobe, culminating in the anterior temporal pole. Perceptual and low-level visual properties of the objects were reflected by posterior occipito-temporal activity (BA 19). Semantic conceptual properties of the

object, which are necessary to categorize objects in semantic meaningful groups, were suggested to be located in the anterior temporal lobe.

It is thus now widely accepted that object recognition involves a pathway along the ventral visual stream. The processing of the visual information is extremely rapid, starting from the retina and the LGN, proceeding from V1, V2 and V4 to posterior to anterior temporal cortices. The inferior temporal cortex is proposed to play a crucial role in object recognition (DiCarlo et al., 2012). The entire neural time course of object recognition as suggested by DiCarlo et al. (2012) is illustrated in Figure 2.1.

Tasks which involve categorization, identification and motor responses are considered to additionally involve prefrontal cortices (Riesenhuber & Poggio, 2000). In particular, the ventromedial prefrontal cortices are considered to provide long-term memory functions which may facilitate recognizing familiar objects (Akirav & Maroun, 2006). The ventrolateral and ventromedial cortices, presumably with a left hemispheric dominance, are proposed to guide top-down retrieval of knowledge from long-term memory and to guide the selection of target items among competitors (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005). Furthermore, the ventromedial cortex – also referred to as orbitofrontal cortex (OFC) – was found to peak earlier than the inferior temporal cortex, which was interpreted to indicate that OFC activity was crucial of successful recognition earlier than activity in the visual cortex, and suggest to support the critical prediction that the OFC provides semantic information which facilitates visual object recognition (Bar et al., 2006). Finally, higher-level conceptual associations, providing a fine-grained semantic analysis, are supposed to be processed in more anterior ventral temporal regions (Bonner & Price, 2013; Clarke et al., 2012).

In the present study, in the Picture-Word Interference task, colourful, but simple pictures of everyday objects or animals are presented and named by the participant, while irrelevant distractor words have to be ignored. Hence, object recognition, and more particular, the labelling and naming of pictures, was essential for solving the task. Consequently, said frontal and temporal brain regions which are proposed to support object recognition, are also expected to be involved in the picture naming task.

Chapter 3

Word Production

To induce cognitive conflicts, in the present study, two Stroop-like tasks were used. In both paradigms the participant was instructed to name objects or quantities overtly. Hence, single word production was a crucial part of the cognitive process investigated, therefore a brief summary of its processing stages and its neural substrates will now be presented.

The following Chapter 4 on *Cognitive Conflicts* (see p. 33 ff.) will discuss the Number Stroop task and the Object Stroop task.

3.1 Cognitive Processes

There is little disagreement regarding the major stages of word production, even though some relevant issues about the dynamics of the speech production process remain controversial.

It is general consensus that the input to the word production system comes from a conceptual processing stage, in which the **concept** of the intended message is formed. The concept can either be part of a larger message or simple, like the concept of an object which is derived from a line drawing (Levelt, 1999). At the conceptual stage, for example, the object 'mango' is perceived and its concept is activated. The concept units are connected to word units in the subsequent stage. Nodes in higher representation levels activate nodes in lower representation levels through a spreading-activation mechanism (Dell, 1986; Levelt, 1999).

Furthermore, converging evidence, for instance, from the tip-of-the-tongue phenomenon (Vigliocco, Antonini, & Garrett, 1997), from brain lesion studies and speech error analyses (Dell, Schwartz, Martin, Saffran, & Gagnon, 1997) or from various picture-word interference investigations (e.g. Schriefers et al., 1990) has led to the conclusion that lexical selection involves the processing of two separate stages:

In the first stage, the concept-to-be-lexicalized is mapped to a corresponding abstract lexical node. The stage is referred to as **lemma representation** (Dell & O'Seaghdha, 1992; Levelt, 1989). The lexical node points to the syntactical features of the word, namely, for instance, its gender, grammatical class or number, but it does not include phonological information. For example, after the lexical concept 'mango' is activated as the target, activation spreads to its corresponding lemma. In the semantic network, not only the target, but also related concepts and their corresponding lemmas, e.g. 'pineapple', 'banana', and 'kiwi', may receive activation. Activation spreads through the network and the most highly activated node is selected (Dell & O'Seaghdha, 1992; Levelt, 1999; Roelofs, 2002). However, the hypothesis of the lemma as an abstract node has been challenged by Caramazza (1997).

Information about the words' phonology, on the other hand, is represented by a separate stage, which is referred to as **word form representation**. It provides a link to the phonological features of the word, for instance, the phonemes /m/ /ae/ /ŋ/ /g/ /ɔʊ/. The encoding of the phonemes proceeds in a particular order, i.e. from left to right (Dell, 1986; Levelt, 1999). According to Levelt (1999), the access of the words' phonological code is subsequently followed by a rapid syllabification and prosodification. A phoneme-level representation is also referred to as 'lexeme' (Levelt, 1992; Morsella & Miozzo, 2002).

Finally, to execute **articulation**, a sequence of motor programs is activated (Hickok, 2014; Mädebach, Oppermann, Hantsch, Curda, & Jescheniak, 2011; Morsella & Miozzo, 2002; Paucke, Oppermann, Koch, & Jescheniak, 2015). The articulatory output is suggested to be monitored by the speaker (Levelt et al., 1991).

Hence, there is little disagreement regarding the main stages of the speech production process.

Still, some issues about the dynamics and the architecture of the word production process, mainly regarding the two stages of lexical representation, remain controversial. One open question concerns the capacity limitations of the process (Paucke et al., 2015).

Another topic of much research is the question whether the flow of information is strictly serial and all-or-none (Levelt, 1989) or whether activation is cascading and proceeds automatically (Dell, 1986).

3.2 Neural Substrates

In the present study, either quantities or objects are named. Simultaneously with the target number or the target object, distractor words are presented. Distractor words are considered to influence the naming of a target, because words cannot be ignored, they must be read and processed.

I'll therefore begin with a brief overview on the neural correlates of language processing in general, which also involves word reading. In the subsequent paragraph I'll focus on the production of words, in particular on overt naming.

3.2.1 Neurobiology of Single Word Processing

An early neurobiological model on the processing of single words was the *Wernicke-Geschwind Model*, which was established by Carl Wernicke (*1848) and later modified by Norman Geschwind (*1946). Even though its conclusions were drawn from a limited number of cases - namely lesion studies - it already offered depictions of the key functions of Broca's and Wernicke's area and aphasia.

According to the model, for hearing and repeating a word - for instance the first word in the headline, 'neurobiology' - initially, the sound is processed by the auditory system, but it cannot be understood until it reaches Wernicke's area via the *arcuate fasciculus*. For repeating, hence, articulating the word, the information must be conveyed back to Broca's area and finally to the motor cortex to create the muscular movements which are required for speaking (cf. Bear et al., 2007, p. 620 ff.).

For over one hundred years, this model was the basis of our knowledge on the neurobiology of language processing, until non-invasive brain imaging techniques like EEG and fMRI became available for research. From then on, language processes could be investigated with healthy human beings during normal functioning. Obviously, the technical innovations led to an incredible increase in spatial and temporal resolution.

For instance, one of the key nodes of language processing - Broca's area - is now considered to be composed of several subregions, which presumably also serve different functions. For example, Amunts et al. (2010) introduced twelve anatomical subregions of Broca's area (Amunts et al., 2010, p. 8, fig. 9 and 10). And Goucha and Friederici (2015) recently investigated two subregions of Broca's area in detail: Brodmann area 44 and 45. The authors conclude that Area 44 might be functionally specialised in the processing of mere syntactical information.

Meanwhile, not only several regions and subregions, but also different pathways have been identified between them. According to Friederici (2012) and Friederici and Gierhan (2013), four fibre tracts - two dorsal and two ventral - connect the key nodes necessary for language processing. The corresponding neural circuit thus connects the regions that are relevant for language. To begin with, reading recruits the visual system and listening involves the auditory system. Subsequently, also other language-related areas are involved. These include the inferior frontal cortex, comprising Broca's area, and the superior temporal cortex, including Wernicke's area, parts of the middle temporal gyrus (MTG) and the inferior parietal and Angular Gyrus in the parietal lobe. For language production, also motor and premotor cortices are activated.

If someone is reading a word - for instance the word 'neurobiology' in the headline - according to Friederici (2012) the input comes from the visual word form area in the fusiform gyrus (FG). If you consider that someone is reading the word 'neurobiology' to you, the acoustic-phonological information is processed in the left middle portion of the superior temporal gyrus (STG) which includes the primary auditory cortex (PAC). The information is conveyed on a ventral pathway to the STG, anterior to Heschl's gyrus (BA 41 and 42), where the entire word form is considered to be processed. Amazingly, after only 50 to 80 ms you seem to be able to recognize that you are confronted with a word (and not a pseudoword). Also the words' syntactic category information is already present after 40 to 90 ms. About 120 - 150 ms later, an early automatic phrase structure building process in the anterior STG starts. Therefore, also basic syntactic processes are considered to follow a ventral stream including the frontal operculum (FOP) and superior parts of Broca's area, namely pars opercularis (BA 44). Semantic

processes, in particular, lexical-semantic access and semantic judgements and categorization on word-level, are processed in inferior parts of Broca's area, namely pars triangularis (BA 45) and pars orbitalis (BA 47) (Friederici, 2012; Friederici & Gierhan, 2013).

Ventrally, the frontal and the temporal cortex are connected by two pathways which may serve different functions. First, basic syntactic processes are considered to follow the uncinate fascile (UF), which connects the anterior inferior frontal cortex with the anterior temporal cortex. Second, semantic processes and comprehension are supported by the inferior-fronto-occipital fascile (IFOF), also known as extreme capsule fiber system (ECFS), which provides a link between frontal and occipital parts of the brain, also incorporating parietal and temporal areas. Lexical-semantic information is processed in the left middle temporal gyrus (MTG). When decoding more words of a sentence - e.g. 'neurobiology of' - and thus going beyond single word processing, also other parts of the brain, namely the anterior and posterior superior temporal lobe and Angular Gyrus are supposedly involved (Friederici & Gierhan, 2013).

The semantic processing therefore appears to follow ventral pathways which connect inferior frontal regions, in particular BA 45 and BA 47, with temporal, parietal and occipital cortices. In cases where the processing of phonological information requires the support from working memory, for instance, to hold a word, the intraparietal sulcus (IPS) seems to be involved (Friederici, 2012; Friederici & Gierhan, 2013; Makuuchi & Friederici, 2013). Working memory supporting the processing of syntactical information, is proposed to involve frontal regions, namely the left inferior frontal sulcus (LIFS) (Makuuchi, Bahlmann, Anwander, & Friederici, 2009).

For semantic processing, a widely distributed left lateralized network is involved which connects temporal with parietal and frontal regions.

3.2.2 Neurobiology of Single Word Production

At the beginning of the chapter, the different stages of the word production process have been laid out, now, their corresponding neural correlates will be outlined. As aforementioned, in the present study participants had to read words and name line drawings overtly, for that reason, the following introduction on single word production will be confined to word reading and picture naming.

Similar to the language processing network presented earlier, the neural substrates of the core processes of speech production are also dominant in the left hemispheric temporal and frontal regions, extending to the inferior parietal cortex. In particular, the main neural substrates for the production of single words are located in the left inferior frontal, middle and superior temporal cortex.

perceptual and conceptual encoding Effects regarding visual perceptual processes seem to occur early, around 95 to 150 ms after a picture or a word are presented. Subsequently, for pictures, after around 200 ms, conceptual information seems to be available (Di Russo et al., 2002; Schendan & Lucia, 2010; see also Chapter 2.2.3 'Object recognition', p. 23 ff.).

Even though there are similarities in the perceptual and conceptual processing of word reading and picture naming, the tasks also differ in some aspects: First, initially, the neural correlates for the recognition of words and objects overlap, but subsequently, they diverge. Second, according to Indefrey (2011), conceptual information is retrieved for picture naming, but not word reading.

According to Price (2012), visually presented words and pictures are extracted, integrated and represented according to their visual features and patterns. These processes are assumed to involve the left ventral occipital gyrus. For the processing of familiar visual forms, anterior parts of the ventral occipital gyrus have been identified. Visual word form processing is associated with the left MTG and Angular Gyrus (Price, 2012) and in particular with the left fusiform gyrus, which is supposed to host the Visual Word Form area (Cohen et al., 2002).

Again, conceptual processing is assumed to be restricted to picture naming, and not active for word reading tasks (Indefrey, 2011). According to Price (2010), the conceptual processing in speech production relies on the same regions which are associated with single-word comprehension by Binder, Desai, Graves, and Conant (2009). Hence, conceptual preparation is proposed to involve a large left hemispheric network, which includes inferior parietal, inferior and middle temporal regions, dorsomedial and ventromedial prefrontal cortices comprising the inferior frontal gyrus, as well as the parahippocampal and posterior cingulate gyrus (Binder et al., 2009; Indefrey, 2011; Price, 2010).

In particular the left Angular Gyrus is assumed to occupy "a position at the top of a processing hierarchy underlying concept retrieval and conceptual integration" (Binder et al., 2009, p. 2776). It is proposed to play a crucial role in the integration of complex information and the retrieval of knowledge. The left dorsomedial prefrontal cortex (DMPFC) is considered to guide goal-directed retrieval of semantic

information, in particular, if the response has to be selected from a large set of alternatives (Binder et al., 2009).

lemma selection and word-form retrieval For conceptually driven lemma retrieval, which is the next step in the picture naming process, only one region, namely the mid section of the left middle temporal gyrus (MTG) was identified. Arguably, it is not involved in phonological encoding (Indefrey & Levelt, 2004; Indefrey, 2011).

For the production of words, either for picture naming or word reading, but not for generating pseudowords, the phonological word-form is retrieved. This process seems to cause enhanced activity in the left posterior superior temporal gyrus (STG).

Phonological encoding also includes syllabification, which is considered to activate the left inferior frontal gyrus (IFG), namely, Broca's area (Indefrey, 2011). According to Abel et al. (2011), late phonological processing is related to bilateral pars opercularis (BA 44), the finding results from a brain connectivity study on overt picture naming with right-handed, left-handed and ambidextrous participants.

The assumption that the left MTG, STG and IFG are indeed highly relevant for successful word production, was also confirmed in a study using transcranial magnetic stimulation (TMS) during overt picture naming by Schuhmann, Schiller, Goebel, and Sack (2011). TMS was applied 150, 225, 300, 400, and 525 ms after the picture was presented. Increased picture naming latencies for TMS on the midsection of the left MTG were observed 225 and 400 ms after the picture was presented. An effect of TMS on the left IFG (Broca's area) was observed after 300 ms only. Finally, the left posterior STG (Wernicke's area) was sensitive to TMS 400 ms after the picture was presented. The findings indicate that the three left hemispheric brain regions are indeed essential for picture naming, apparently they are contributing to different temporal stages of the process.

According to Price (2012), word retrieval (but not conceptual or articulatory processing) is strongly associated with activation in the left anterior prefrontal cortex, including pars triangularis (BA 45) and BA 46. When distracting semantic information is presented, word retrieval becomes more semantically demanding. In this particular case, the medial superior frontal cortex and the ventral inferior frontal cortex (pars orbitalis, BA 47) are involved. Moreover, enhanced activity is also found in the left Angular Gyrus/inferior parietal cortex, left ventrolateral temporal cortex and left hippocampus.

In the context of phonological interference - as opposed to semantic interference - activity in the left temporo-parietal junction is reported, which is interpreted to be caused by a heightened demand in verbal self-monitoring (Price, 2012). This assumption is convergent with the findings from Makuuchi and Friederici (2013), regarding the parietal localisation of the phonological working memory, which was mentioned earlier.

articulation In general, articulatory planning is assumed to involve the left anterior insula (Indefrey, 2011), eventually comprising both hemispheres (Price, 2012). Presumably, the anterior insula supports the control of breathing during overt articulation (Koelsch et al., 2009). The final overt responses seem to activate the left precentral gyrus or supplementary motor area (SMA), left thalamus and the cerebellum (Indefrey, 2011; Price, 2012). The articulatory network may also include the Cingulate Cortex, its anterior zone is also associated with response suppression (Price, 2012).

left hemispheric dominance Apparently, the brain areas involved in language processing and language production are predominant in the left hemisphere. For example, according to Indefrey (2011), nearly the entire word production network for picture naming and word generation is located in the left hemisphere, more specifically, in the left IFG, precentral gyrus, SMA, mid and posterior STG, MTG, fusiform gyrus, insula, thalamus and cerebellum. The right hemisphere seems to only involve the mid STG.

For semantic processing, according to Binder et al. (2009), the dominance of the left hemisphere was 'moderate' with 68% of all foci being left lateralized. Still, only some 'weak' activations in the right hemisphere are mentioned in their meta-analysis, these are found in the right Angular Gyrus, the posterior MTG, and the posterior cingulate gyrus (Binder et al., 2009, p. 2271).

So far, we have seen convergent evidence for neural structures subserving the different stages of the word production process. **Perceptual** processing was found to activate ventral-occipital regions (Binder et al., 2009). **Conceptual** processing involves a wide network in parietal, temporal and prefrontal areas (Binder et al., 2009; Indefrey, 2011). Regions involved in **lemma selection** and **word-form retrieval** include the (mid section of the) left middle temporal gyrus (MTG) (Maess, Friederici, Damian, Meyer,

& Levelt, 2002; Friederici, 2012; Indefrey & Levelt, 2004; Indefrey, 2011; Schuhmann et al., 2011), the left superior temporal gyrus (STG) (Indefrey, 2011; Schuhmann et al., 2011) and left inferior frontal gyrus (IFG) (Indefrey, 2011; Price, 2012; Schuhmann et al., 2011). The anterior insula is involved in articulatory planning, **response** execution is supported by the SMA, left thalamus, cerebellum (Indefrey, 2011; Price, 2012).

Currently, neurolinguistic research trends to specify the network both anatomically and functionally, aiming to provide a fine-grained network of the regions, subregions, as well as connections involved in speech comprehension and production.

Chapter 4

Cognitive Conflict

To gain cognitive control, we have to update our information and inhibit distracting influences. Selecting actions and controlling our behaviour allows us to live in accordance with the external world and our internal goals. Flexible and adaptive behaviour thus requires a balance of initiation and inhibition of our operations. For instance, sometimes a dominant response must be suppressed in favour of an appropriate one. Cognitive control thus refers to our ability to successfully perform tasks in situations in which we have to solve such a conflict (Cieslik et al., 2015; Kim, Chung, & Kim, 2010; Neubert, Mars, & Rushworth, 2013).

Hence, the Stroop Paradigm (Stroop, 1935) is a frequently used method to investigate cognitive control. It can be used to examine conflicts between relevant and irrelevant stimuli.

4.1 Stroop as a Measurement for Cognitive Conflict

It all started with the early finding of Cattell (1886), who measured the reaction times for the naming of objects and colour patches, as well as the reaction times for the reading of words and letters. He observed that "[t]he time was found to be about the same (over 1/2 sec.) for colours as for pictures, and about twice as long as for words and letters" (Cattell, 1886, p. 65). He reasoned that the reaction time differences could be explained by the fact that reading words and letters happens automatically, whereas naming objects and colours requires some effort.

Stroop (1935) combined the naming of colour patches with word reading. He was interested in the question of how the reading of colour words interfered with the naming of colour patches and whether practice had an influence on the interference effect. The original finding was that naming the ink colour of a word was severely hindered when the word referred to another colour, e.g., when the participant had to name the ink colour of the word 'RED' printed in blue compared to the naming of colour patches (Stroop, 1935, Exp. 1). Comparatively, word reading was hardly influenced by the ink colour, e.g., reading the word 'RED' printed in blue (Stroop, 1935, Exp. 2).

Given the robustness of the Stroop Colour-Word Test, together with its simplicity and ease of administration, it is not surprising that the task has become a widely used tool for the experimental investigation of interference, attention and, more generally, to test cognitive control.

In his review on the Stroop paradigm from 1991, MacLeod states that the set of articles on the Stroop effect has exceeded 700. Meanwhile (2015), i.e. 80 years after Stroop published his landmark article, a search on Google Scholar (https://google.scholar.de) results in 4.200 articles which include the word 'Stroop' in their title, and a search on Google Books Ngram Viewer (https://books.google.com/ngrams) shows that the frequency of the word 'Stroop' in the English literature is constantly rising since 1935.

Meanwhile, numerous variations of the original Colour-Stroop task have been developed. Figure 4.1 illustrates six examples. The paradigms displayed in panel (b) and (c) were used in the present study. In all variations the subject is instructed to name a target and to ignore the dominant but irrelevant distractor.

There are several attempts to explain the nature of the Stroop conflict. One of them, the so called *automaticity hypothesis* was already mentioned by Cattell (1886). It accounts for the asymmetry of the Stroop conflict, namely, that words interfere with colour naming, but colour naming does not interfere with word reading. This hypothesis suggests that the reading of the word is automatized but the naming of the colour is not. Therefore, naming the colour takes more effort and draws more attentional resources.

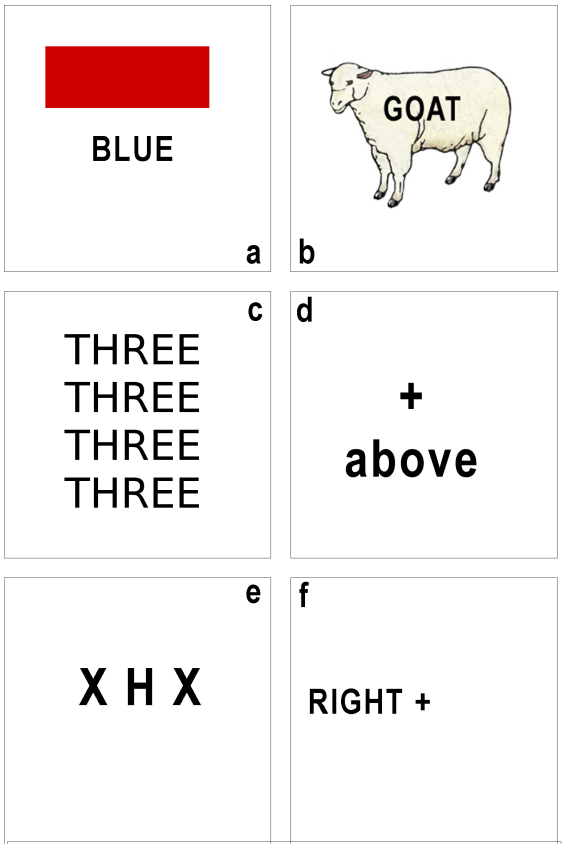


Figure 4.1: Six variants of the Stroop task, image modified from MacLeod and MacDonald (2000, p. 384). All examples illustrate the incongruent or related condition, which evokes interference. (a) Original Stroop task ('name colour patch') (b) Picture-Word Interference task ('name picture') (c) Numerical Stroop task ('count number words') (d) Spatial Stroop task ('press button according to position') (e) Flanker task ('press button if H is detected') (f) Simon task ('press left button if target word on the left side')

A similar assumption, which is compatible with the automaticity view, is the *relative speed of processing* hypothesis. It begins with the fact that the reading of words is faster than the naming of colours. The difference in speed results in two potential responses, an irrelevant word, which comes first, and the relevant colour, which follows, and both compete for being selected. The competition, or interference, causes the time costs. According to MacLeod (1991), the three key assumptions of the hypothesis are, first, that both dimensions are processed in parallel, but with a different speed, second, they terminate in a response buffer with a limited capacity, and third, the speed is also influenced by other factors, such as the nature of preceding trials and other elements of the response set.

In another hypothesis, which was also introduced by MacLeod (1991), the source of the conflict is not attributed to the response stage but rather to the perceptual phase of the processing. The basic idea is that the incongruent information of the word interferes with the early, perceptual encoding of the colour information.

Also Seymour (1977) argued that the Stroop conflict occurs early, before the response stage, but not on a perceptual level, rather in the semantic system. In particular, the incongruent colour word and the ink colour were assumed to activate similar, but incompatible semantic codes.

How cognitive conflicts in the Stroop paradigm emerge, when they arise and where they are located, remain open questions.

Several variations of the paradigms have frequently been used to examine a wide range of questions regarding how, when and where conflicts are processed, but with very different thematic priorities. Accordingly, another critical question is how the findings from the different variants relate to each other.

For instance, a long-standing debate is concerned with the question whether the Stroop effect in the Picture-Word Interference (PWI) task and the Colour-Word Stroop task are two manifestations of the same process. First, the prototypical procedure is identical in both paradigms: the participant is requested to respond to the target and to ignore an irrelevant distractor word. Second, also the latency distributions are similar for both tasks: when target and distractor relate to different but related concepts, interference effects are observed. When both refer to the same concept, naming is facilitated. The effects disappear, when the task is changed to naming the written word (*Stroop asynchrony*). Accordingly, some researchers have argued that the limitations of the cognitive system in the PWI and the Stroop are

analogous (MacLeod, 1991; Piai, Roelofs, & Schriefers, 2014; Schnur & Martin, 2012), however, others have assumed that they differ (Dell'Acqua, Pesciarelli, Jolicœur, Eimer, & Peressotti, 2007; Van Maanen & Van Rijn, 2008; Van Maanen et al., 2009). Finally, Van Maanen and Van Rijn (2008) and Van Maanen and Van Rijn (2008) have suggested that temporal differences can be explained with a single cognitive process underlying both tasks. According to them, they rely on the stimulus type (i.e. novel pictures vs. simple colours) and can be traced back to their retrieval from declarative memory (Van Maanen & Van Rijn, 2008; Van Maanen et al., 2009). (For more details on the debate, see Chapter 4.1.2 'Stroop with Objects'.)

Evidently, it is not yet known at which level or which levels along the processing stream the distracting information causes a conflict. Furthermore, it is unclear, whether different stimulus types result in distinct cognitive limitations or processes.

In the present study, these questions were addressed with two different Stroop-like paradigms, namely, a Stroop task with numbers and a Stroop task with objects (Picture-Word Interference task).

4.1.1 Stroop with Numbers

In the Numerical Stroop paradigm, a target number and an irrelevant magnitude are activated simultaneously. The latter is expected to interfere with the relevant response.

The target as well as the distracting number can be expressed with different number notations, e.g. with Arabic numerals, with number words in all kinds of languages or with dot patterns.

In some of the Number Stroop variations, for instance in the number-size congruity paradigm, the target and the distractor number are presented simultaneously, i.e. the irrelevant number is presented next to the relevant number, which must be chosen on the basis of its physical or numerical size. Sometimes, only one number is presented, and the target must be compared to a reference number such as '5', which is announced at the beginning of the experiment (e.g. Ratinckx & Brysbaert, 2002).

In another variation, the so-called Counting Stroop task, which was also used in the present study, the quantity of identical (number) words is counted and the irrelevant word must be ignored (e.g. Bush, Whalen, Shin, & Rauch, 2006). In addition to a congruent condition (e.g. the number '2' presented twice) and an incongruent condition (e.g. the number '3' presented twice), also a neutral condition may be used (e.g. the noun 'dog' presented twice).

In the so-called decade-unit-digit task, in addition to the overall magnitude difference, also the congruency of the unit digit and the decade is manipulated.

In the literature on the Numerical Stroop task, the terms *stroop effect*, *interference effect* and *congruency effect* are used synonymously. The terms refer to the conflict that occurs between the relevant and the irrelevant information and is either captured by comparing the incongruent to a congruent, a neutral or control condition.

Behavioural Findings

A huge variety of research questions has been addressed with the Number Stroop task.

For instance, the Counting Stroop task can be used to examine the nature and the time course of cognitive conflicts in numerical processing (e.g. Bush et al., 1998; Pagano & Mazza, 2013). With this paradigm, typically, a robust congruency and distance effect is observed. The effect seems to be independent of number notation. In this task, a behavioural congruency effect was, for instance, observed for Arabic digits (Pagano & Mazza, 2013), English number words (Bush et al., 1998) or Chinese Kanji number words (Fan, Gau, & Chou, 2014). In the Chinese Counting Stroop by Fan et al. (2014), participants counted four Kanji number symbols. Kanji symbols corresponding to English 'it', 'human', 'understand' and 'no' served as a control condition. The control symbols were matched to the digit condition in terms of the number of syllables, the strokes per sign (visual complexity) and the frequency.

Some variations of the Numerical Stroop task were designed to address more specific questions regarding numerical processing. They were, for instance, used to examine how binary digits are processed ('decade-unit-digit congruency'; Liu, Wang, Corbly, Zhang, & Joseph, 2006), to explore how numerical size interferes with physical size and vice versa (Ansari, Fugelsang, Dhital, & Venkatraman, 2006; Algom, Dekel, & Pansky, 1996; Kaufmann et al., 2005; Szűcs & Soltész, 2012), to investigate hemispheric differences in the processing of number (Ratinckx & Brysbaert, 2002), to examine whether number processing is divergent for different notations (Ischebeck, 2003; Ratinckx & Brysbaert, 2002) and if numbers automatically activate magnitude representations (Ischebeck, 2003; Fias, Reynvoet, & Brysbaert, 2001; Wong & Szűcs, 2013). In addition to manipulating the presence or absence of an irrelevant number ('congruency

effect'), also the influence of the numerical proximity between the relevant and the irrelevant magnitude can be explored ('numerical distance effect').

For instance, in the decade-unit-digit Stroop task (e.g. Liu et al., 2006), the participant has to perform magnitude judgements on two-digit numbers. The numbers' decades and unit digits are either congruent (e.g. 21 vs. 39, with 2<3 and 1<9) or incongruent (e.g. 33 vs. 51, with 3<5 but 3>1). The task allows distinction between the impact of the magnitude difference and the congruency of the decade and the unit digit and to examine whether binary digits are processed holistically. In the study by Liu et al. (2006) decade-unit digit incongruency was reported to influence naming latencies, therefore, binary digits were interpreted to be processed one at a time and not as an entity.

In the number-size congruity paradigm, the cognitive conflict is caused by a mismatch between the numerical magnitude and the physical size of the number. In this paradigm, magnitude comparisons are performed on single digits and the numerical size and the physical size of the number are either congruent (e.g. 9 vs. 3), incongruent (e.g. 3 vs. 9) or neutral (e.g. 3 vs. 3). The paradigm does not only enable to examine comparison abilities for numerical magnitudes, but also for physical size with the identical material across two tasks. Therefore, it can be used to compare the cognitive mechanisms underlying symbolic and non-symbolic comparative judgements (Algom et al., 1996; Kaufmann et al., 2005; Szűcs & Soltész, 2012; Tang, Critchley, Glaser, Dolan, & Butterworth, 2006). In number-size congruity paradigms, typically, the incongruent, but irrelevant physical magnitude is reported to interfere with numerical judgements, and numerical magnitudes interfere with physical comparisons.

A behavioural size-congruency effect has been obtained with Arabic digits (Kaufmann et al., 2005; Szűcs & Soltész, 2012; Tang et al., 2006) and with number words (Ansari et al., 2006).

The distance effect is typically observed for the task-relevant dimension; i.e. for numerical comparisons, a numerical distance effect is found (Ansari et al., 2006; Kaufmann et al., 2005; Pinel et al., 2004) and for physical comparisons, a physical distance effect is reported (Kaufmann et al., 2005; Pinel et al., 2004). However, in a study by Tang et al. (2006), a distance effect was also observed for the task-irrelevant dimension.

But according to Algom et al. (1996), the number-size-congruency effect is only obtained when the discriminability of the numerical size and the physical size is mismatched, with the more salient dimension intruding on the less discriminable dimension. Algom et al. (1996) point out that in most studies, other than the numerical size, the physical size is often much more pronounced and manipulated with a large deviance (e.g. Ansari et al., 2006; Tang et al., 2006). According to Algom et al. (1996), for nearly matched dimensions, number and size were separable and did not interfere.

Reportedly, the number-size-congruency effect is reduced when the distractor is presented repeatedly. To investigate the sequence effect, in a study by Cohen Kadosh, Gevers, and Notebaert (2011) three sequential presentations of two congruency conditions in a size-digit comparison task were manipulated. The magnitude of the digit 1, 4, 6 or 9 was compared to the reference number 5. The physical size was either small or large, and either congruent or incongruent with the numerical magnitude. The sequence was either congruent (e.g. 1 followed by 4, both smaller than reference number), identical (e.g. 1 followed by 1) or incongruent (e.g. 4 followed by 6, the digits required different responses regarding the reference number). Reportedly, the congruency effect was not present when the irrelevant dimension was presented repeatedly (same and identical condition). Cohen Kadosh et al. (2011) argue that the finding is supposed to provide evidence for the 'Response-suppression' hypothesis, according to which the initial suppression of the distractor sustains.

Interhemispheric interactions of the integration of number information were investigated behaviourally by Ratinckx and Brysbaert (2002) in a numerical Stroop task with Arabic digits and number words. Both notations, the digit-digit as well as the digit-number word Stroop, elicited a response compatibility, a congruency, a numerical distance and a SNARC effect. However, number processing did not differ for the hemifields, suggesting that both hemispheres represent numerical magnitude information. In the study by Ratinckx and Brysbaert (2002), the Arabic digits 1 - 3 and 5 - 7 or the corresponding number words (in Dutch) were compared to the reference number 4. To test for the hemispheric differences, the computer screen was split with two vertical lines, which left a small gap in between. The subject was instructed to fixate the gap. An arrow, which was presented in the gap, pointed to the target. The subject had to respond with a button press whether the target number was smaller or larger than the reference number 4. The distractor was presented in the opposite hemifield. In the digit-digit as well as the digit-word condition, the participants were faster when target and distractor yielded the same response (e.g. small | small), than when it asked for different responses ('response compatibility'). They

were faster for identical numbers (e.g. 1 | 1), compared to different numbers (e.g. 1 | 2) ('congruency effect'). They were faster for the extreme values (e.g. 1 or 7) compared to the near values (e.g. 3 or 5) ('numerical distance effect'). In addition, responses were faster when the small number was presented in the left hemifield and the larger number was presented in the right hemifield ('SNARC effect') (Ratinckx & Brysbaert, 2002).

Apparently, in the study by Ratinckx and Brysbaert (2002), incongruent Arabic digits interfere with judgements on digits as well as on number words. The authors report that the influence of number words on the naming of digits was not included in their study, because a pilot study had indicated that number words did not interfere with Arabic digits.

This comment leads to the question whether distinct number notations are processed differently by the reader, or, more specifically, if digits and number words both automatically activate their magnitude code.

Unlike Ratinckx and Brysbaert (2002), in a number naming task by Ischebeck (2003), not only incongruent digits are reported to interfere with the naming of (Dutch) number words, but apparently number words also interfere with the naming of digits. The digits and the number words were presented next to each other. Overall, number words were named faster than digits. In both tasks, a congruency effect was detected, which means that the naming of digits as well as of number words was faster in the congruent condition (e.g. 1 - one; two - 2) than in the incongruent condition (e.g. 1 - two; one - 2), but the effect was greater for digit targets with word flankers. For digit targets with number words, also a distance effect was observed, but it was not present for number word targets with digit distractors. Ischebeck (2003) therefore suggests that number words do automatically activate an abstract representation of their numerical magnitude. The greater effects for distracting number words are compatible with the 'preferred format hypothesis' (e.g. 'triple-code model' by Dehaene & Cohen, 1996), according to which number words are the preferred format for a naming task, whereas digits have to be translated.

Indeed, digits are not consistently found to automatically activate magnitude representations. For instance, in a same-different task by Fias et al. (2001), the processing of Arabic digits and number words were compared. Half of his participants had to read single Arabic digits (e.g. 8) and ignore a simultaneously presented number word which could either be congruent (e.g. "eight") or incongruent (e.g. "seven"). Likewise, the other half had to read number words ("eight") and to ignore the corresponding Arabic digit. Because incongruent number words interfered with digit naming, but incongruent digits did not interfere with word reading, the results were interpreted to show that 'digits are processed like pictures' (Fias et al., 2001).

Also in a digit-digit comparison task by Wong and Szűcs (2013), numerical incongruence did not influence reaction times, but, apparently, visual similarity did. In their study, adults and children (10-11 years) had to judge the visual similarity of two simultaneously presented single digits. Visual resemblance was quantified on the basis of four functions and numerical similarity on the basis of three functions. For example, for the perceptual function P_C, the overlapping lines in digital seven-segment displays were calculated, and the perceptual function P_{SA} was based on subjective visual similarity ratings. Linear regression models showed that none of the *numerical* similarity functions predicted the reaction times (RTs) of adults and children. For the visual similarity, the childrens' RTs were significantly influenced only by P_C and the adults RTs only by P_{SA}. Wong and Szűcs (2013) conclude that digits do not automatically activate magnitude representations, neither in adults nor in children.

Neuronal Localisation

To localise the source of the conflict in the Numerical Stroop task, neurophysiological measures such as EEG and fMRI have been used.

Most of these studies were conducted with the number-size congruity paradigm, because it allows to model the influence of numerical and physical size all at once. Even if both dimensions were employed, for the sake of simplicity, the following results only include the numerical comparison task. As mentioned, for the numerical version of the task, the participant is instructed to compare the magnitude of two numbers and to ignore their physical size.

Several ERP studies have aimed to identify the succession of events in the conflict processing of the Numerical Stroop task. For instance, the question whether interference results from perceptual difficulties or if it is caused by a later processing stage was addressed with the number-size congruity paradigm by Szűcs and Soltész (2012) and with the Counting Stroop task by Pagano and Mazza (2013).

In the study by Szűcs and Soltész (2012), subjects were instructed to compare two simultaneously presented digits regarding their physical size or magnitude. To manipulate the response conflict, half of the incongruent and congruent number-size combinations were preceded by an effective cue, which

was pointing to the correct direction, or a neutral cue (no direction). The physical size distance was either small (45 vs. 50 points) or large (40 vs. 50 points), and the numerical distance was either 1 or 7. Reaction times as well as the P300 showed congruency effects. However, even though significant reaction time differences led to the conclusion that the conflict was higher in the neutrally cued trials, the N450, which was considered a robust marker of the Stroop conflict, did not differ for the cued and the uncued condition. Consequently, the Stroop conflict was related to stimulus conflict detection or resolution and not to the response stage.

Pagano and Mazza (2013) obtained similar results with the Counting Stroop task. In their study, congruency effects were observed 400 to 600 ms post-stimulus and interpreted to occur at the retrieval stage and not at the perceptual stage. In their ERP study, one to four digits were counted, which were either congruent (e.g. four 4s) or incongruent (e.g three 4s) with the quantity. The digits were presented equally to the left or the right side of a fixation cross. The digits were uniquely coloured in either red or green, and the randomly distributed letter A (in the opposite colour) served as a distractor. The response was made by button press on one of four vertically aligned buttons. Because the early N2pc amplitudes (190 - 290 ms post-stimulus) increased as a function of target numerosity but were little affected by congruency it was concluded that individuation during subitizing occurs at a perceptual stage. A late negativity, 400 - 600 ms post-stimulus, which was modulated by numerosity as well as congruency, suggested that number semantic is processed at later stages.

Most of the functional imaging studies with the Number Stroop paradigm are conducted to address two theoretical issues: First, the neural basis of the conflict between task-irrelevant and task-relevant information is investigated, and second, it is used to address the neural network associated with the processing of magnitude.

The first question compares incongruent and congruent (or neutral trials). For the second issue, in most studies, numerical distance effects are supposed to show that the processing of the magnitude has gone beyond a coarse categorization and to illustrate numerical processing despite of its task-relevance.

Even for different variations of the Numerical Stroop task, i.e. for the number-size congruity paradigm (Ansari et al., 2006; Kaufmann et al., 2005; Tang et al., 2006), for the decade-unit congruity task (Liu et al., 2006) and for the Counting Stroop (Bush et al., 1998), the interference effect (incongruent > congruent trials) is consistently associated with activity in frontal areas, in particular, in the right middle frontal gyrus (Ansari et al., 2006; Bush et al., 1998; Kaufmann et al., 2005; Liu et al., 2006; Tang et al., 2006).

For the numerical distance effect, enhanced activity in the bilateral inferior parietal gyri was observed (Ansari et al., 2006; Kaufmann et al., 2005; Liu et al., 2006, but see Tang et al., 2006).

According to Ansari et al. (2006) and Kaufmann et al. (2005), the differences in the activation patterns suggest some degree of independence between numerical processing and congruency effects.

The number-size congruity paradigms were conducted with number words (Ansari et al., 2006) and Arabic digits (Kaufmann et al., 2005; Tang et al., 2006).

For instance, in the study by Ansari et al. (2006), number words ranging from 'one' to 'nine', were displayed either in a small (30 point) or large (58 point) font size (e.g. congruent: one TWO, incongruent: ONE two, neutral: one two). For the numerical distance effect, the trials were divided in those with small (1-3) and large (5-7) distances. The subjects were instructed to chose the numerically larger digit.

In the study by Kaufmann et al. (2005), six Arabic digits were used to create digit pairs, which were presented in three different sizes. The two numerical distances 1 and 4 were realised. Finally, in the study by Tang et al. (2006) nine different physical sizes were used to create four numerical and four physical distances. In the study by Kaufmann et al. (2005) and Tang et al. (2006), physical as well as numerical comparison were performed.

For number words and digits, a numerical distance effect (NDE) was observed, but it was only present for large effects (small > large distances). The NDE was associated with activity in the bilateral inferior parietal sulcus and left insula (Ansari et al., 2006; Kaufmann et al., 2005). However, Tang et al. (2006) did not find any evidence suggesting that the parietal cortex was modulated by either numerical or physical distance.

For number-size incongruent trials, some brain regions were frequently found active, but none of the regions were consistently found active in all studies. In particular, number-size interference was reflected by enhanced activity in the right inferior parietal lobe and precuneus (Ansari et al., 2006; Kaufmann et al., 2005), right middle frontal and superior frontal lobe (Ansari et al., 2006; Tang et al., 2006), in the inferior frontal lobe (Kaufmann et al., 2005; Tang et al., 2006), thalamus (Ansari et al., 2006; Tang et

al., 2006) and claustrum (Ansari et al., 2006; Kaufmann et al., 2005).

Activity in the anterior and posterior cingulate gyrus, right insula and left paracentral lobe was only observed in the study with verbal material (Ansari et al., 2006). The number-size congruity paradigms with digits elicited activity in the right precentral gyrus (Kaufmann et al., 2005) and right superior parietal and left superior frontal gyrus (Tang et al., 2006).

Finally, activity in the right middle and superior frontal gyrus was also observed for incongruent compared to neutral trials in the Counting Stroop paradigm by Bush et al. (1998). In their study, either number words or common nouns (animals) were counted, hence, the quantity and the word was either incongruent or neutral. The authors report activity in the bilateral middle frontal gyrus (BA 9/46), in the anterior cingulate (BA 24), left precentral (BA 4), left superior frontal gyrus (BA 6) and superior parietal cortex (BA 7). In addition, right hemispheric inferior temporal activity (BA 37) was found.

To sum up, the bilateral inferior parietal gyri seem to reflect *numerical distance* effects for digits and number words (Ansari et al., 2006; Kaufmann et al., 2005). A parametrically modulated distance effect was not observed (Tang et al., 2006), instead, a numerical distance effect was only observed when small distances were compared to large distances (Ansari et al., 2006; Kaufmann et al., 2005).

Even for different variations of the Numerical Stroop task, the *conflict* between the numerically relevant and the irrelevant information (incongruent > control condition) was consistently associated with activity in right frontal areas, in particular, in middle frontal gyri (Ansari et al., 2006; Bush et al., 1998; Kaufmann et al., 2005; Tang et al., 2006) and inferior frontal gyri (Kaufmann et al., 2005; Tang et al., 2006). In addition, enhanced activity in the ACC (Ansari et al., 2006; Bush et al., 1998), the right inferior parietal (Ansari et al., 2006; Kaufmann et al., 2005) and superior parietal lobe (Bush et al., 1998; Tang et al., 2006) was observed.

Because congruency effects are associated with fronto-parietal areas, whereas numerical processing is restricted to the parietal cortices, Ansari et al. (2006) and Kaufmann et al. (2005) suggest that the activation patterns of numerical versus conflict processing show some degree of independence.

4.1.2 Stroop with Objects

In an Object Stroop task, participants are typically instructed to name the picture of an object, while trying to ignore an irrelevant distractor picture or distractor word which is superimposed on the target picture.

These types of task are also referred to as 'Picture-Picture Interference task' (PPI) or 'Picture-Word Interference task' (PWI) (Meyer & Damian, 2007).

Like other Stroop-like tasks, such as the Colour-Word Stroop and Number Stroop task, also Object Stroop tasks are typically used to investigate cognitive conflicts, which are supposed to shed light on capacity limitations and attention allocation in the processing of simultaneously activated items (Fagot & Pashler, 1992).

The Picture-*Picture* Interference task, for instance, has been used to investigate perceptual interference effects (Damian & Bowers, 2003). The Picture-*Word* Interference task, on the other hand, allows to investigate the influence of a distracting word on the picture naming process, and has thus become one of the most often used paradigms for the investigation of lexical access in single word production.

To induce a cognitive conflict, the relatedness of the picture and the distractor may be manipulated. For instance, the distractor can either be identical with the picture (e.g. pictured 'dog', word: 'dog'), semantically related (e.g. pictured 'dog, word: 'cat') or unrelated (pictured 'dog', word: 'hat'). Related distractors typically slow down picture naming compared to identical distractors, a finding which is analogue to the results from the Colour-Word Stroop task (Stroop, 1935). This effect is often termed *Stroop(-like) effect*. Furthermore, related distractors also slow down picture naming compared to unrelated distractors, which is referred to as *semantic interference effect*.

As mentioned at the beginning of the chapter, the Colour-Word Stroop task and the Picture-Word Interference task show similar reaction time patterns, but it is still an open issue, whether the conflicts in the Picture-Word and the Color-Word paradigm share the same origin. According to MacLeod (1991, p. 168), this "is not a straightforward problem given the different sorts of questions being addressed in the two domains".

Early publications on the Colour-Word Task as well as the Picture-Word Interference task were conducted to investigate the locus and the nature of a 'central attentional bottleneck', which is observed

when two tasks are performed concurrently (e.g. Fagot & Pashler, 1992).

Findings from the PWI were thus used to contribute to the ongoing debate whether the Stroop effect occurs at an early or a late processing stage. The debate stands in the tradition of the discussion on the locus of the Colour-Word Stroop task (MacLeod, 1991).

As mentioned previously, the location of the cognitive conflict in the performance of the Stroop task was either assigned to the early processing stages of perceptual and semantic encoding or to late processing stages regarding response selection or response execution (Dell'Acqua, Job, et al., 2007; Roelofs, 2003).

Models of single word production, on the other hand, assume processing stages of conceptual encoding, lemma retrieval, word-form encoding and articulation (Levelt et al., 1999; Roelofs, 2003) (cf. Chapter 3 on 'Word production'). Early selection in models of Stroop task performance correspond to lexical selection in models of picture naming, whereas late selection corresponds to word-form encoding, and finally, response execution is assumed to correspond to articulation (Piai, Roelofs, & van der Meij, 2012).

Recently, the 'Picture-Word Interference task' (PWI) is thus mostly employed to investigate how we resolve conflicts during speech production. The findings are supposed to shed light on general attentional capacity limitations, but also, more particular, to constrictions regarding the time course of single word production, as well as the neural correlates of the speech production process.

Behavioural Findings

The Picture-Word Interference task has mainly been used to examine two different topics: as mentioned in Chapter 3 on 'Word production', it was used to contribute to an ongoing debate regarding the architecture and the dynamics of the word production process.

Second, as mentioned at the beginning of the present chapter, it was used to investigate whether the Picture-Word Interference effect and the Colour-Word Stroop effect originate from the same capacity limitations. The latter question was mainly investigated in the context of dual-task paradigms.

word production The question, whether semantic interference was located at a perceptual level – as proposed earlier (Dell'Acqua, Job, et al., 2007) – or at a lexical level, was investigated by Damian and Bowers (2003). They compared interference effects in a Picture-Picture Interference (PPI) and Picture-Word Interference (PWI) task. Damian and Bowers (2003) argued, if the conflict was located at a perceptual or conceptual level, it should be observed in the Picture-Picture Interference task, but if it was not located at an early processing stage, it should only be obtained for the Picture-Word Interference task. Because the interference effect was only observed for the PWI, and not for the PPI, the results were interpreted to indicate that the interference effect did not originate from a perceptual or conceptual processing stage.

Meanwhile, the debate regarding capacity limitations in the speech production process has narrowed down to the question of whether lexical selection is competitive or not.

Because words can only be produced one by one, obviously, at least one bottleneck is situated at the articulation stage of the speech production process. For proponents of the 'Response Exclusion hypothesis', this bottleneck is relevant, because according to their assumptions, phonological encoding takes place automatically, for all, even unsolicited, lexical items. Hence, lexical selection is not competitive, but the relevant response competes for being selected prior to articulation (e.g. Janssen et al., 2008; Morsella & Miozzo, 2002).

For proponents of the 'Lexical selection by competition hypothesis' (LSC) the articulatory bottleneck is irrelevant. According to their assumptions, lexical selection is completed before the phonological encoding phase starts. If, and only if, the lexical node has received the highest activation and has thus 'won' the competition at the lexical selection phase, it is selected and encoded. Consequently, the competition is terminated after the lexical selection phase and does not affect later stages of the speech production process (Levelt et al., 1991; Schriefers et al., 1990).

The 'semantic interference effect' in the PWI is interpreted to reflect lexical competition, and the task has thus become one of the most often used paradigms for the investigation of lexical access in word production.

To get an insight in the succession of the speech production stages interference in the PWI is often manipulated with SOAs. For instance, in the PWI study by Schriefers et al. (1990), semantic interference for related picture-word combinations (e.g. pictured 'dog', word: cat) was only observed when the related

word was presented 150 ms before the picture. Facilitation effects for phonologically related words (e.g. pictured 'dog', word: fog), were only found if the word was either presented simultaneously with the picture (SOA 0 ms) or 150 ms after the picture. Schriefers et al. (1990) have therefore concluded that the lexical selection phase and the phonological encoding phase proceed in two serially ordered steps, which do not interact, which is in line with the assumptions from the LSC account.

Investigations of the semantic context effect distinguish between categorical relations (e.g. pictured 'dog', distractor word: cat), phonological relations ('dog' - fog), part-whole relations ('dog' - tail), associative relations ('dog' - bone), and sometimes also functional relations ('dog' - leash) and congruency ('dog' - dog).

Compared to unrelated distractor words, categorical relations typically increase picture naming latencies, when presented at short SOAs (Abel, Dressel, Weiller, & Huber, 2012; Dell'Acqua et al., 2010; De Zubicaray, Wilson, McMahon, & Muthiah, 2001; Diaz et al., 2014; Piai et al., 2012; Schnur et al., 2009); this effect is referred to as 'semantic interference effect' (Schriefers et al., 1990).

However, picture naming is reported to be facilitated in the context of functional or part-whole relations (Muehlhaus et al., 2014; Diaz et al., 2014), for associative relations (Abel et al., 2012; De Zubicaray, Hansen, & McMahon, 2013), for congruent distractors (Piai et al., 2012), and for phonological relations (Abel et al., 2012; Diaz et al., 2014; Dell'Acqua et al., 2010).

For current models of speech production, the different effects were difficult to integrate. Typically, according to the LSC account, semantic interference is interpreted to reflect lexical competition, because semantically related distractor words increase the activation level of the competing lexical nodes (Levelt et al., 1999). With this assumption, it is difficult to explain, why spreading activation should be restricted to categorical relations and why it should not affect, e.g., associative or part-whole relations.

In order to integrate the findings in the context of an LSC account, Abdel Rahman and Melinger (2009) have recently proposed a 'swinging lexical network' theory. According to the authors all effects inside the network result from a 'trade-off' between conceptual facilitation and lexical competition. In general, all semantically related distractors facilitate selection from the network, unless a categorical cohort is large enough to induce lexical competition. Only in this case, the interference effect is assumed to outweigh facilitation (Abdel Rahman & Melinger, 2009).

Stroop vs. PWI To investigate attention allocation, the Picture-Word Interference task has been used in the context of dual-task experiments. In principle, dual-task manipulations are conducted to create an attentional overload, which is supposed to illuminate capacity limitations of the attentional process.

In a typical dual-task experiment, the subject has to give two responses. Reaction times are recorded for both responses (e.g. RT1 and RT2). The input for the two responses is presented subsequently. For instance, first a tone (T1) is presented and second a PWI task (T2). The temporal gap between the two inputs, i.e. the stimulus onset asynchrony (SOA), is manipulated. If a person tries to perform two tasks at the same time or with a fast succession, i.e. at a short SOA, the response to the second stimulus typically becomes slower. The increased reaction time for the second response is often termed 'psychological refractory period' (PRP) or PRP effect (Pashler, 1994).

The psychological refractory period paradigm was used to investigate whether the Stroop effect in the Colour-Stroop task and the semantic interference effect in the PWI may be located at the same attentional bottleneck or not (Fagot & Pashler, 1992; Dell'Acqua, Job, et al., 2007; Schnur & Martin, 2012; Piai et al., 2014).

After conducting a series of dual-task experiments, Fagot and Pashler (1992) came to the conclusion that the Stroop effect was located at a 'late' attentional bottleneck, i.e. during the response selection or response execution. In one of their experiments, Fagot and Pashler (1992, Experiment 7) instructed participants to give a manual response (button press) as well as a vocal response. The first task was a tone discrimination task (high vs. low, Task 1), which was followed by a Stroop Colour-Word task (Task 2). Both tasks were separated with the SOAs -50ms (Task 2 before Task 1), +50ms, +150ms and +450ms (Task 1 before Task 2). Fagot and Pashler (1992) reported that the reaction times of the incongruent compared to the congruent Stroop condition were 'additive', that is, the magnitude of the effect did not differ for short and long SOAs. They concluded from the results that the Stroop effect was located at the response-selection or response-execution stage, and that it was not located at a perceptual stage.

In a similar experiment by Dell'Acqua, Job, et al. (2007) the same question was investigated for the PWI, i.e. the semantic interference effect. Again, participants had to identify a tone. The first task was then followed by a PWI, at varying SOAs ranging from 100 ms to 1000 ms. The first response was given manually. For the second task, the participants had to name a picture while ignoring a semantically

related or unrelated word. Dell'Acqua, Job, et al. (2007) report that the semantic interference effect was not present at short SOAs (RT difference between related - unrelated condition: -7ms), but semantic interference grew larger at long SOAs (difference: +68ms). Because the semantic interference effect was not observed at short SOAs, it was concluded that the conflict had been resolved during the perceptual stage of the first task (Dell'Acqua, Job, et al., 2007). Semantic interference was thus interpreted to occur during the perceptual encoding stage, and therefore, it differed from the location of the Stroop effect, which had been attributed to the response selection stage by Fagot and Pashler (1992). Dell'Acqua, Job, et al. (2007) concluded from the findings that the semantic interference effect is not a Stroop effect.

However, the findings by Dell'Acqua, Job, et al. (2007) could not be replicated (Piai et al., 2014; Schnur & Martin, 2012). For instance, Schnur and Martin (2012) conducted two dual-task experiments with the same material and experimental design as used by Dell'Acqua, Job, et al. (2007), with the only difference that the trial order randomization differed and the material was translated from Dutch to English. Unlike Dell'Acqua, Job, et al. (2007), Schnur and Martin (2012) found semantic interference effects for the PWI at both, short and long SOAs, following tone discrimination. Arguably, the findings are in line with the results from Fagot and Pashler (1992), suggesting that semantic competition occurs at the point of response selection or later, implying that semantic interference in the PWI is a post-perceptual effect.

Schnur and Martin (2012) conclude that the patterns of the semantic interference effect for PWI and the Stroop effect (Fagot & Pashler, 1992) do not differ, suggesting that both effects involve response selection or response execution mechanisms.

Neuronal Localisation

To test for the time course and the neural correlates of the conflicts induced by different semantic relations, numerous studies with the Picture-Word Interference task were conducted.

The question whether the Stroop effect and the semantic interference effect are located at the same processing stages was pursued in an ERP study by Piai et al. (2012). Participants performed a PWI task with overt naming, and the pictures of common objects were paired with either identical, semantically related or unrelated distractor words (in Dutch). For the unrelated condition, the words from the related condition were redistributed. In addition, the frequency of the pictures was manipulated (e.g. high: 'arm', 'bed', low: 'banana', 'cup'). The Stroop effect was reflected by a significant negativity (ERP) between 250 and 500 ms, starting at fronto-central areas, proceeding to centro-parietal regions. A different electrophysiological effect, namely a 'time-frequency representation' (TFR), a significant relative power increase in the beta band, also between 230 ms and 370 ms, was observed for the semantic interference effect. The results were interpreted to reflect a processing at the lexical selection stage for the Stroop effect as well as for semantic interference. The electrophysiological difference between the Stroop effect and the semantic interference effect is interpreted to reflect a functional difference in attentional control, not temporal differences.

In a similar ERP study by Dell'Acqua et al. (2010), the question was narrowed down to the succession of the lexical access stages, namely, lexical selection and phonological encoding. Consequently, the pictures were not only combined with related and unrelated distractor words, but also with phonologically related words. In the latter condition, the distractor word shared the two initial phonemes with the picture name (in Spanish). The effects for the semantic condition were observed at 106 ms to 320 ms, and reportedly confined to left temporal and frontal regions. For the phonological condition, on the other hand, a later and gradual increase in activity was observed in the same regions, which was extending to temporo-occipito-parietal areas in the right hemisphere. The fact that semantically related distractor words caused a fast effect (100 ms post picture onset) was interpreted to indicate and 'ultra-fast' processing of semantic information, which was assumed to cause a regulatory feedback to whole-word phonological representations.

Several studies used functional imaging to test for the cognitive architecture mediating the interference effects. Interestingly, even if, for instance, categorical, phonological or associative picture-word combinations lead to fundamentally different reaction time patterns, the resulting effects seem to rely on a highly replicable neuronal network, mainly comprising the left middle temporal gyrus (MTG) and left inferior frontal gyrus (IFG).

According to the results from an early study with fMRI by De Zubicaray et al. (2001), for instance, interference was found to activate brain areas which were arguably involved in lexical retrieval and phonological encoding. The findings led to the conclusion, that interference involves both processing stages and that both stages interact. In their study, related distractors were contrasted with a control condition (a row of XXXX) in an overt picture-naming task. Lexical retrieval was predicted to involve

the left middle temporal cortex, phonological encoding, on the other hand, was presumed to activate left posterior superior and middle temporal gyri. In addition to activity in these temporal cortices, also anterior cingulate and bilateral medial and superior frontal cortices were found active. Activity of the latter was interpreted to indicate inhibitory control, which was assumed to reflect the need to suppress the unsolicited response.

Schnur et al. (2009) report that enhanced activity in the left temporal cortex is not only reflecting a categorically related context, but also a phonologically related context. On the other hand, a semantic, but not phonological, context effect was reflected by enhanced activity in the left inferior frontal gyrus (Broca's area). In their fMRI study, Schnur et al. (2009) manipulated the context of the picture to be named. Pictures were presented in a 'blocked naming paradigm' along with either semantically related pictures (e.g. truck, car, bike), mixed-category items (e.g. truck, foot, dog) or phonologically related items, which were sharing the same initial phoneme (e.g. bear, belt, bird). Compared to the mixed category items, picture naming was slower in the semantic context and faster in the phonological context.

The results were confined by Abel et al. (2012), using categorically related, associatively related, phonologically related as well as unrelated distractor words in a picture-naming paradigm. Auditory distractor words were presented 200 ms before the picture. Semantic interference (categorical>unrelated) was reported to activate the left inferior/middle frontal gyrus (BA 11/47), this area was also active for phonologically related distractors. Convergent activity for phonologically related and associatively related distractor words, on the other hand, was observed in the left middle temporal gyrus (BA 21), as well as left superior and inferior parietal lobe (BA 7/40). Activity in the right temporal gyrus (BA 21) was only found for phonologically related distractor words.

Left MTG activity was also obtained by Muehlhaus et al. (2014) with functionally related picture-word pairs (e.g., 'flute'-note) and part-whole related picture-word pairs, (e.g., 'bike'-handlebars) compared to unrelated picture-word pairs. The conjunction of the two conditions found additional left parietal and supramarginal activity. Functional (>unrelated) pairs also elicited right parahippocampal activity, part-whole (>unrelated) trials showed left supramarginal activity.

Finally, left middle temporal and left supra-marginal activity was observed for part-whole distractors (> unrelated) in a classical PWI by Diaz et al. (2014), in which coloured line drawings and were presented with superimposed words. Phonologically related (> unrelated) distractors were reported to elicit enhanced activity in bilateral supra-marginal and Angular Gyrus. The categorical and the unrelated condition did not differ significantly (Diaz et al., 2014).

Obviously, there is a fundamental difference for the picture naming latencies in the context of categorically related, compared to associative, functional, part-whole and phonologically related distractor words: the categorical condition typically leads to increased reaction times, whereas the other conditions are consistently reported to facilitate picture naming (Abel et al., 2012; Dell'Acqua et al., 2010; De Zubicaray et al., 2001; Diaz et al., 2014; Muehlhaus et al., 2014; Piai et al., 2012; Schnur et al., 2009; De Zubicaray et al., 2001).

Apparently, one region in the left inferior parietal (BA 40) and supramarginal lobe was consistently associated with facilitated picture naming. Activity in this region was observed for phonological (Abel et al., 2012; Diaz et al., 2014) and associative (Abel et al., 2012), as well as for functional (Muehlhaus et al., 2014) and part-whole distractors (Diaz et al., 2014; Muehlhaus et al., 2014)[1].

On the other hand, the left middle temporal gyrus (Abel et al., 2012; De Zubicaray et al., 2001; Diaz et al., 2014; Schnur et al., 2009; Muehlhaus et al., 2014), left inferior temporal gyrus (Diaz et al., 2014; De Zubicaray, Johnson, Howard, & McMahon, 2014) and the left inferior and middle frontal gyrus (Abel et al., 2012; Schnur et al., 2009) seem to constitute a neural substrate for both, interference and facilitation effects: Left middle temporal (MTG) activity was elicited in the context of semantic/categorical (De Zubicaray et al., 2001; Schnur et al., 2009), phonological (Abel et al., 2012; Schnur et al., 2009), associative (Abel et al., 2012), functional (Muehlhaus et al., 2014) and part-whole related distractors (Diaz et al., 2014; Muehlhaus et al., 2014). Posterior temporal activity (extending to the Angular Gyrus) was found for part-whole related (Diaz et al., 2014), phonological distractors (Diaz et al., 2014), for semantically related distractors (Kotz, Cappa, von Cramon, & Friederici, 2002), as well as for categorically homogeneous compared to heterogeneous blocked cycles (De Zubicaray et al., 2014).

Activity of the left inferior frontal gyrus (LIFG), on the other hand, was observed for the semantic/categorical (Abel et al., 2012; Schnur et al., 2009) and phonological condition (Abel et al., 2012, but see Schnur et al., 2009).

[1] All results were obtained by contrasting the critical condition with an unrelated or control condition.

Chapter 5

Behavioural Experiments

5.1 Numerical Stroop Paradigm

5.1.1 Introduction

I carried out two numerical Stroop tasks[1] 1. with immediate naming and 2. with delayed naming.

Task-irrelevant information can interfere with a task. This was already demonstrated by Stroop (1935), who showed that naming the ink colour of a word was more error-prone and slower when the word was a conflicting colour word, for example, the word BLUE printed in red. The meaning of the colour word, the *distractor*, was irrelevant but could not be ignored and thus interfered with naming the ink colour (cf. Chapter 4 *Cognitive Conflict*).

In the numerical Stroop task, different quantities of identical numbers are counted, and the meaning of the number word is supposed to influence the counting procedure. The quantity and the meaning of the number word(s) are either congruent or incongruent. Furthermore, in a neutral condition, common nouns, e.g. 'house' or 'animal', are counted.

The incongruent number is supposed to interfere with the counting process. The difficulty is expected to decrease with increasing numerical distance between target and distractor (*numerical distance effect*, Moyer & Landauer, 1967). The nouns in the neutral condition reflect the influence of distracting information which is not interrelated with counting (cf. Chapter 2.1 *Numbers*).

In the first experiment, the impact of the distractor word in the Numerical Stroop task is investigated. The subject is instructed to count words and respond orally. Filler trials with pseudo words are supposed to urge the subject to process the meaning of the word.

In the present study, the locus of the Stroop conflict in the mental processing stream is of particular interest. Much debate centres around whether the locus of the conflict may be attributed to perceptual or semantic input effects (Sturz et al., 2013; Luo, 1999), to response output effects (Fagot & Pashler, 1992; Dell'Acqua, Job, et al., 2007; Van Maanen & Van Rijn, 2008; Van Maanen et al., 2009) or a combination of the two (De Houwer, 2003; Chen et al., 2013; Schmidt & Cheesman, 2005; Zhang & Kornblum, 1998).

One way to distinguish between the semantic-perceptual and the response stage, and to be able to investigate the locus of the interference effect, is to test whether the effect is still observed when participants delay their responses. In a delayed naming paradigm, the naming of the target is postponed, and naming latencies are thus supposed to reflect the bottleneck at the response level. If interference occurs at the response stage, it should be observable in a delayed naming paradigm (Janssen et al., 2008).

Also in the delayed version of the present Numerical Stroop task, one to six identical (number) words were presented and had to be counted, and after a short temporal delay a cue was presented. The correct response depended on the colour of the cue, therefore, both the quantity of the word(s) and the meaning had to be retrieved and stored and the subject had to postpone the response until the cue was shown. According to the colour of the cue either the quantity or the word had to be expressed.

The delayed naming paradigm was first observed behaviourally and subsequently investigated with fMRI (Chapter 6).

[1] Furthermore, to investigate the impact of the notation, two delayed numerical Stroop tasks with Arabic digits and number words were accomplished. In addition, an immediate naming Stroop task with red catch trials was conducted. The findings of these experiments did not differ from those presented in the chapter. Consequently, they will not be discussed.

To adjust the timing of the trial to the particular requirements of fMRI, and thus to be able to capture blood flow modulations, which are peaking several seconds after exposure, the trials were elongated to a total duration of twelve seconds and the interval between the stimulus and the cue was varied.

5.1.2 Methods

Participants

Overall, 38 participants were recruited using the subject database PESA. Due to technical reasons, two participants were excluded (Exp. 1). The final sample consisted of 36 participants, who were distributed as follows across the experiments: Exp. 1: 28 participants (22 women), mean age 23.93 (SD = 3.11, range = 20-31); Exp. 2: 8 participants (6 women), mean age 23.25 (SD = 2.25, range = 21-28)[2].

Materials

For each trial, a set of identical (number) words was presented. The quantity of the number(s) ranged from one to six. The number(s) and the quantity could either be congruent, incongruent or unrelated (neutral condition). Because only one of six number-quantity combinations was congruent, all congruent items were presented three times.

The experiments were conducted in German. The words were presented in capitals. In the neutral condition, common nouns and not numbers were presented. The neutral items were "Frau" (woman), "Haus" (house), "Mann" (man) and "Tier" (animal). The frequency of the number words and the common nouns was matched using the (German) Corpus Portal for Search in Monolingual Corpora ('Wortschatz Lexikon Leipzig') (Quasthoff, Richter, & Biemann, 2006). According to the corpus, the frequency classes of the numerals and the nouns did not differ significantly ($\chi^2 = 8.0, df = 6, p = .24$).

In total, 72 items were presented (18 congruent, 30 incongruent and 24 neutral items). The numbers and words were displayed in columns on a white background within an area sized 15mm x 70mm max. The length of the column was dependent on the quantity of the numbers. The experiments started with a practice block, this material was not part of the stimulus set.

Exp. 1: Immediate Naming Paradigm In addition to the 72 experimental items, 24 catch trials (pseudo words) were used. The pseudo words for the catch trials were created by changing the onset of each German numeral of the stimulus set in such a way that the resulting word appeared to be an actual German word, but had no meaning, i.e.: "kins", "swei", "grei", "rier", "tuenf", "fechs". Consequently, the pseudo words had exactly the same length as the numerals and were extremely similar in their appearance. Due to the close phonological and orthographic resemblance of the pseudo words and the number words, the participants were expected to process the stimuli more carefully.

Every pseudo word was presented four times to each participant.

The experiment started with 18 (incongruent) practice trials, which were not part of the stimulus material. The practice trials consisted of the German number words "null" (zero), "sieben" (seven), "neun" (nine), "zehn" (ten) and three catch trials with the pseudo words "batze", "polk" and "zand".

Exp. 2: Delayed Naming Paradigm The 72 items from Experiment 1 were presented as experimental items, i.e., followed by a blue cue which meant that participants had to respond with the quantity of the word(s). In addition, 48 filler items (6 congruent, 18 incongruent and 24 neutral) were presented with a red cue, meaning that participants had to respond with the word itself.

Because the experiment was supposed to serve as a pilot study for the fMRI experiments, null trials were also included (see Chapter 6.1). For the null trials, only the fixation cross and a blank screen was shown.

The practice trial consisted of 11 experimental items, 3 null trials and 8 filler items in a randomized order. They were not part of the stimulus material.

Procedure

Each participant was tested individually in a session lasting about 15 min. The participant was seated in a dimly lit room, separated from the experimenter by a partition wall. In both sessions, variations of the Picture-Word Interference task were also conducted. The order of the Numerical Stroop experiment and the Picture-Word Interference task was counterbalanced across participants.

[2]The second experiment is a pilot study for the fMRI experiment in Chapter 6.

After the participants signed the informed consent, they were shown the instruction. The instruction consisted of a picture showing an example for a target, which was not part of the stimulus material. The experiment then started with a practice block. The rate of catch trials in the actual experiment was always lower than in the practice block.

The participants' responses were recorded and the response onsets were measured starting either from stimulus onset (Exp. 1) or cue onset (Exp. 2). Finally, voice key triggers were manually corrected with Checkvocal (Protopapas, 2007).

Responses were coded as erroneous and excluded from the analysis for the following reasons: subject response started too early, i.e. before cue or stimulus were shown or after the cue had disappeared. Responses were also excluded when a distractor was named in the experimental condition or the number was counted in the filler condition. Also miscounted answers, stutterings and missed responses were excluded from the analysis.

Subsequently, all reaction times faster than 100 ms or longer than 1800 ms were treated as outliers and removed.

Exp. 1: Immediate Naming Paradigm The participant was instructed to respond immediately after the stimulus was presented but to remain silent if the words did not exist in German (i.e. a pseudo word). Again, catch trials were included to ensure that the stimuli were processed carefully by the participant, i.e. forcing them to avoid strategies such as an intentional blurring of vision.

A trial always started with a blank screen presented for 200 ms followed by a fixation cross, which was presented for 500 ms on the centre of the screen. This was followed by another blank screen, which was presented either for 600 ms or 900 ms. The duration of the blank screen slightly varied to avoid monotony and the participants' expectancy of the stimulus. Then the target, i.e. a column of identical number words (either congruent or incongruent with the quantity), of common nouns (neutral condition) or pseudo words (catch trials), appeared for 500 ms and the voice key trigger was activated simultaneously. The participants' responses were recorded and the response onsets were measured.

Exp. 2: Delayed Naming Paradigm The participant was instructed to memorize the number and the quantity and to withhold the response until a cue was shown. The colour of the cue indicated the response to be given. The blue cue indicated to respond with the quantity, the red cue indicated to utter the word.

Six temporal trial variations were used, adding up to a total trial duration of twelve seconds (see Appendix, Table A.3). First, a fixation cross was presented for 0.5 seconds, then a blank screen for 0.5 to 2 s in intervals of 0.5 s. Then the stimulus was presented for 0.5 s. Subsequently, a blank screen was presented for 3.5 to 5.5 s. The cue was displayed for 2 s. The last blank screen was presented for 1.5 to 5 s.

Apparatus

The experiments were programmed with Presentation® software (Version 0.70, www.neurobs.com). The experiments were conducted on an Intel Pentium® 4 CPU 3.06GHz computer with a Belinea 17 inch TFT monitor. Spoken responses were recorded with a Sennheisser PC131 headset microphone on a SoundMAX Digital Audio sound device. Finally, voice key triggers were manually corrected using the Checkvocal tool for DMDX (Protopapas, 2007).

5.1.3 Results

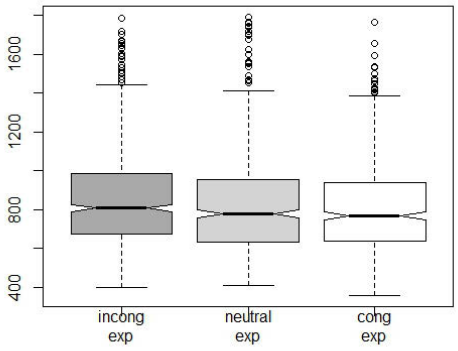
The data of the immediate as well as the delayed naming paradigm were analysed with linear mixed effect models using the package *lme4* (Bates, Mächler, Bolker, & Walker, 2015) in *R* (Version 3.0.2) (R Core Team, 2014), with the random factor participant and the fixed factor condition and quantity (i.e. the quantity of the words to be counted). In the delayed naming paradigm, in addition to the factor condition, the factor cue and the interaction were investigated. Usually, reaction times are not normally distributed, but rather show a positive skew. This was also true for the distribution of the reaction times in the present data sets. To transform the reaction times into a normal distribution, the variable was logarithmized. In a second step, separate models for the data of the immediate as well as the delayed naming paradigm were fitted for *absolute distance*. In these models, only the data of the incongruent condition were included. The LME was fitted with the random factor *participant* and the fixed factor *absolute distance*. Post-hoc tests for the interaction term were performed with Least Square Means.

Exp. 1: Immediate Naming Paradigm

The *condition* (congruent, incongruent, neutral) had a significant influence on the naming latency ($\chi^2(2) = 12.79, p < .0001$). For the mean reaction times across condition see Table 5.1. Post hoc tests for *condition* revealed that the reaction times for the counting procedure were significantly longer when quantity and numerals were incongruent compared to the congruent condition (RT difference = 38 ms, $b = -0.04, t(56) = -3.655, p < .01$). They were also longer in the incongruent compared to the neutral condition (RT difference = 21 ms,$b = 0.033, t(56) = 2.743, p < .05$), but the congruent condition and the neutral condition did not differ (RT difference = 17 ms, $b = -0.014, t(56) = -1.070, p = .5$). Also the quantity of the numbers had a significant influence on the naming latency ($\chi^2(3) = 606.32, p < .0001$). For the mean reaction times see Figure 5.5a). Post-hoc tests revealed that the reaction times for one and two items did not differ significantly, $b = -.02, t(5) = -1.32, p = .2$, and they did not differ for one to three items $b = .03, t(5) = 1.63, p = .1$, but for one to four items $b = .13, t(5) = 7.44, p < .0001$, for one to five items $b = .28, t(5) = 16.42, p < .0001$, and for one to six items $b = .36, t(5) = 20.13, p < .0001$, indicating that one to three items could be perceived at a glance, i.e. subitized.

The second model revealed that the *absolute distance* had a marginal influence on the reaction times ($\chi^2(2) = 3.33, p = .067$) (see Figure and Table 5.2).

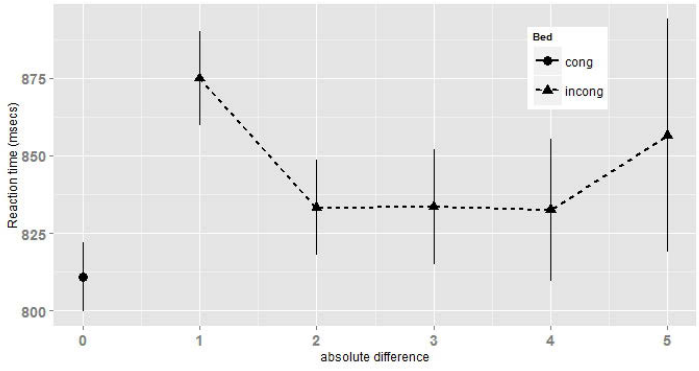
Figure 5.1: Exp. 1: immediate naming paradigm - mean naming latencies across conditions.



condition			
experiment ("count")			
	RT	SD	error
incongruent	849	(241)	2.1%
neutral	828	(260)	1.8%
congruent	811	(245)	0.9%
filler ("remain silent")			
filler	–	(–)	0.5%

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses. RT onsets were determined with Checkvocal (Protopapas, 2007).

Figure 5.2: Exp. 1: immediate naming paradigm - mean naming latencies for absolute distance.



experiment ("count")		
dist	RT	SD
0 (= congruent)	811	(245)
1	875	(252)
2	833	(224)
3	834	(236)
4	833	(229)
5	857	(277)

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses. RT onsets were determined with Checkvocal (Protopapas, 2007).

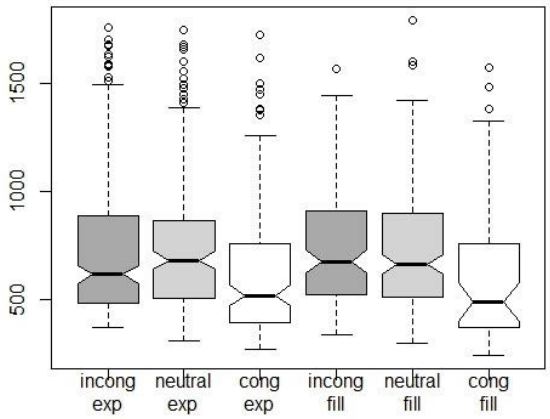
Exp. 2: Delayed Naming Paradigm

Overall, the *condition* did have a statistically significant impact on the naming latencies ($\chi^2(2) = 24.64, p < .0001$). Mean reaction times were longer for reading the number word(s) than for counting their quantity, but the difference was not significant ($\chi^2(3) = .14,\ p = .71$). Also the interaction of *cue* and *condition* was not significant ($\chi^2(4) = 1.79, p = .41$). For the mean reaction times see Table and Figure 5.3.

The *quantity*, i.e. the number of words to be counted, did not have a significant impact on the reaction times ($\chi^2(5) = -0.38, p = .70$), see Figure 5.5b.

Post hoc tests revealed that naming latencies were significantly faster in the congruent condition compared to the incongruent condition both for counting the quantities ($b = 0.17, t(7) = 5.089, p < .01$) and for naming the number (filler trial: $b = 0.23, t(7) = 5.269, p < .01$). Naming latencies were also significantly shorter in the congruent condition compared to the neutral condition both for counting the quantities ($b = 0.18, t(7) = 5.282, p < .01$) and for naming the number (filler trial: $b = 0.19, t(7) = 5.593, p < .01$). Naming latencies for the incongruent condition and the neutral condition did *not* differ, both for counting the quantities ($b = 0.01, t(7) = 0.325, p = 1$) and for naming the numbers (filler trial: $b = 0.004, t(7) = 0.117, p = 1$). The model for *absolute distance* revealed that the factor did not have a significant influence on the reaction time ($\chi^2(2) = 0.14, p = .71$), see Figure and Table 5.4.

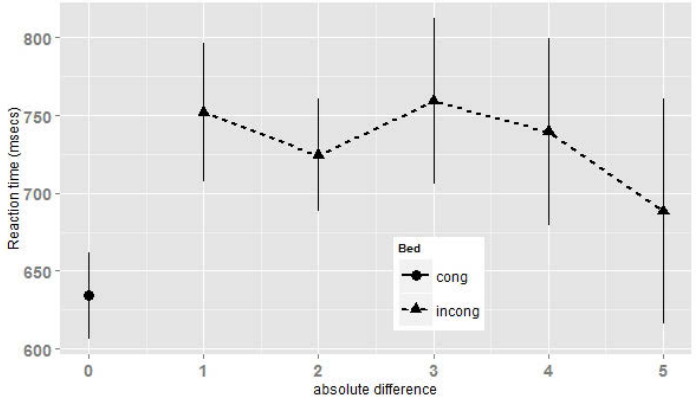
Figure 5.3: Exp. 2: delayed naming paradigm - naming latencies across conditions



condition			
exp ("count")			
	RT	SD	error
incongruent	740	(338)	1.0%
neutral	755	(324)	0.7%
congruent	634	(323)	0.3%
filler ("read")			
incongruent	754	(293)	0.3%
neutral	748	(296)	0.4%
congruent	626	(351)	0.0%

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses, RT onsets were determined with Checkvocal (Protopapas, 2007).

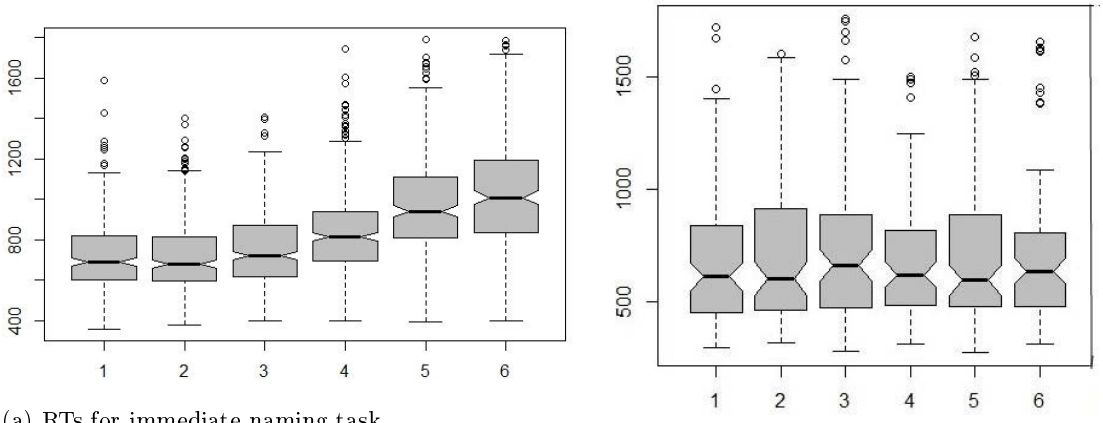
Figure 5.4: Exp. 2: delayed naming paradigm - mean naming latencies for absolute distance



experiment ("count")		
dist	RT	SD
0 (= congruent)	634	(323)
1	752	(384)
2	724	(286)
3	759	(356)
4	739	(334)
5	688	(262)

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses, RT onsets were determined with Checkvocal (Protopapas, 2007). For reasons of clarity, the figure is presented with the standard error of the mean (SEM).

Figure 5.5: Exp. 1 and 2: immediate and delayed naming paradigm - mean naming latencies for quantity



(a) RTs for immediate naming task

(b) RTs for delayed naming task

Mean reaction times (RTs) are given in milliseconds (ms). RT onsets were determined with Checkvocal (Protopapas, 2007).

5.1.4 Discussion

Two temporal variations of the numerical Stroop task were investigated, 1. with immediate naming and 2. with delayed naming.

The Stroop effect is supposed to reflect the impact of the congruency between target and distractor and is captured by comparing the incongruent to the congruent condition. For the interference effect, the incongruent condition is compared to the neutral condition. In the incongruent condition, target and distractor are from the same domain (e.g. 'four four four'), in the neutral condition, they are from different domains and thus unrelated (e.g. 'man man man'). Consequently, the interference effect is supposed to reflect the impact of closely associated, but task-irrelevant information.

In the immediate naming paradigm, in line with expectations, both the incongruent as well as the neutral distractors interfere with the counting procedure, which is reflected by increased naming latencies compared to the congruent condition. Incongruent numbers interfere more than common nouns. In the immediate naming paradigm, therefore, a Stroop effect as well as an interference effect are observed.

In the delayed naming paradigm, again, reaction times (RTs) are increased in the presence of incongruent compared to congruent distractors. Furthermore, RTs are also increased in the neutral compared to the congruent condition. Therefore, a Stroop effect is observed. The increased cognitive demand in the incongruent compared to the congruent condition is supposed to reflect the fact that attentional demands were strongly increased in this condition. In the congruent condition, the quantity and the number were identical, consequently only one dimension of the stimulus needed to be processed and memorized. In the incongruent as well as the neutral condition, both dimensions had to be stored. Because the correct response depended on the colour of the cue, also the origin of the dimension had to be maintained, i.e. whether the number represented the quantity or the word.

In the delayed naming paradigm, incongruent trials did not differ from neutral trials, which means that the interference effect was not observed in the delayed naming paradigm. Consequently, interference does not seem to occur at the response stage.

As one would expect, in the immediate naming task the reaction times increased with the quantity of the target (Figure 5.5a) in other words, the more words were counted, the longer the reaction times. As previously mentioned in Chapter 2.1.2 *Subitizing*, according to Trick and Pylyshyn (1994), fewer than four items are subitized, i.e. perceived within 40 - 100 ms/item, but more than four items have to be counted. This is in line with the results from the present study: in the immediate naming paradigm, reaction times were rapidly increasing for four items. However, in the delayed naming experiment, the reaction times are not increasing with quantity (Figure 5.5b), suggesting that the counting process had been terminated before the response was given.

Contrary to expectations, in the immediate naming paradigm a significant numerical distance effect was not observed. As expected, in the delayed naming paradigm the counting process was terminated, consequently in the delayed paradigm a numerical distance effect was not observed.

5.2 Picture-Word Interference Task

5.2.1 Introduction

I carried out two versions of the Picture-Word Interference (PWI) tasks, 1. with a systematic variation of the stimulus onset asynchrony and 2. with a delayed version of the PWI.

In a Picture-Word Interference paradigm subjects are instructed to name a picture (e.g. 'dog') which is presented together with a word. The word can either be related (e.g. 'dog'-cat), unrelated (e.g. 'dog'-hat) or identical (e.g. 'dog'-dog) with the picture. The word cannot be ignored and is supposed to influence the picture naming latencies. Similarly to the dispute on the locus of the Stroop conflict, the locus of the conflict in the Picture-Word Interference paradigm has been the matter of an extensive debate: According the *lexical selection by competition* hypothesis, interference occurs at the retrieval stage and thus reflects the selection of the target from a set of activated alternatives (Levelt et al., 1999; Roelofs, 1992, 1997; Roelofs & Piai, 2013; Schriefers et al., 1990). According to the *response exclusion* account, on the other hand, interference arises at the response stage, after the lexical selection is terminated, in an articulatory output buffer prior to articulation (Dhooge & Hartsuiker, 2010, 2011; Finkbeiner & Caramazza, 2006; Janssen et al., 2008; Mahon et al., 2007). Again, to investigate the locus of the interference effect, the retrieval stage is separated from the response stage. The investigation centres around whether the effect is still observed when participants delay their responses. In a delayed naming paradigm, the naming of the target is postponed, and naming latencies thus reflect the bottleneck at the response level. If interference occurs at the response stage, it should be observed in a delayed naming paradigm (Janssen et al., 2008). For instance, Janssen et al. (2008) have observed interference in the picture naming paradigm, regardless of whether the distractor word appeared simultaneously with the target (immediate naming) or 1,000 ms after the target picture (delayed naming). Because after 1,000 ms, the retrieval of the picture name was expected to be terminated, target and distractor were interpreted to compete at a late processing stage. However, these findings could not be replicated (Bohle, 2010; Mädebach et al., 2011; Piai, Roelofs, & Schriefers, 2011).

In the first experiment, the 'delay' or stimulus onset asynchrony (SOA) between target picture and distractor word is implemented by segregating the input of the target and the distractor. Hence, the distractor is either presented 100 ms or 50 ms before the picture, simultaneously with, or 50 ms, 100 ms, 150 ms or 200 ms after the target picture.

If the slower dimension - i.e. retrieving the picture name - is given a head start, the participant is supposed to have ample time to retrieve the name of the target before the distractor appears. In this case, the word should not be able to influence lexical processing. Thus, the obtained interference effect is expected not to reflect lexical competition.

In the second experiment, a delayed version of the Picture-Word Interference task, the subject is instructed to name a picture which is presented simultaneously with a distractor word. The distractor word is either related, unrelated or identical with the picture name. The subject is instructed to postpone the response until a cue is shown. The correct response depends on the colour of the cue.

The delayed version of the Picture-Word Interference task was first observed behaviourally and subsequently investigated with fMRI (see Chapter 6.3, pp. 71). Consequently, the timing of the trials is adjusted to the particular requirements of functional MR imaging, the temporal delay between stimulus and cue presentation is varied ('jittered'), and trials are elongated to a total duration of twelve seconds.

5.2.2 Methods

Participants

Overall, 53 participants were recruited using the subject database PESA (Humboldt-Universität Berlin). Due to technical reasons, the data of one participants was excluded (Exp. 1).

The final sample consisted of 52 participants which were distributed as follows across the experiments: Exp. 1: 44 participants (37 women), mean age 25.52 (SD = 2.71, range = 20-30); Exp. 2: 8 participants (6 women), mean age 23.25 (SD = 2.25, range = 21-28)[3].

[3]The second experiment was a pilot study for the functional MR imaging experiment in Chapter 6.

Materials

Two sets with 33 pictures from the picture database by Rossion and Pourtois (2004) were presented in combination with two related and two unrelated distractor words (Exp. 1 and 2) and additionally with the picture name (Exp. 2). For a complete list of the stimulus material, see Appendix, Table A.1 and Table A.2.

In the related condition, distractor words and pictures were (mainly) categorical coordinates (e.g. pictured "bread" with either the word 'cookie' or 'cake'.) For the unrelated condition, the related distractors were randomly assigned to the other pictures of the stimulus set in a way that no semantic or phonological relation with the picture was obtained (e.g. "bread" with 'trophy' or 'violin'). All pictures were presented with two different related and two unrelated distractor words.

Exp.1: SOA variation The two picture sets and the corresponding distractors were alternated and counterbalanced across participants, resulting in 33 related picture-word combinations and 33 unrelated picture-word combinations each.

Fifteen (6%) filler items were randomly chosen from the stimulus material. For the filler trials the distractor word was written in red ink and in this case the picture should not be named (No-Go trials).

Exp.2: delayed naming Only Set B from the picture sets was used (see Appendix, Table A.2). Due to a low naming agreement, the picture "eagle" was replaced by "peacock" and the picture "peach" was replaced by "pear". The distractors were redistributed accordingly.

In addition to the related and the unrelated distractors, the picture was presented together with its name (identical condition).

In total, 165 items were presented to each participant (66 related, 66 unrelated and 33 identical picture-word combinations).

Procedure

For all trials, a white background was used. All experiments were conducted in German.

Exp. 1: SOA variation The participant was instructed to name the picture, but to remain silent if the (distractor) word was written in red.

First, a fixation cross was presented for 500 ms, followed by a blank screen for 500 ms. The distractor word appeared either 100 ms or 50 ms before the picture, simultaneously with the picture (SOA = 0 ms), or 50 ms, 100 ms, 150 ms and 200 ms after the picture. Preexposure of the distractor word is indicated by negative SOA, postexposure of the distractor word is referred to by positive values. The picture was displayed for 2000 ms. The SOA thus ranged from -100 ms to +200 ms in steps of 50 ms.

Half of the participants were assigned to the trials with the SOA -50 ms, 0 ms, +100 ms, +200 ms, the other half with the SOA -100 ms, 0 ms, +50 ms and +150 ms. That implies that the simultaneous presentation (SOA = 0 ms) was processed by all participants. All picture-distractor combinations were counterbalanced and randomized across participants. Consequently, 264 stimuli were presented to each subject (33 *pictures* $\times$ 2 *conditions* $\times$ 4 *SOA*).

Exp. 2: delayed naming The participant was instructed to name the picture if the cue was blue and to read the word in case the cue was red (filler trial).

The timing of the trial was identical to the one described for the Numerical Stroop task, Exp. 2, Chapter 5.1.2 (p. 47), and displayed in the Appendix in Table A.3.

Because the experiment was supposed to serve as a pretest for the fMRI experiments, so-called 'null trials' were also included (see Chapter 6.3). For the null trials, only the fixation cross and a blank screen was displayed.

The practice trial consisted of eleven experimental items, three null trials and eight filler items in a randomized order.

Apparatus

The experiment was programmed with either DMDX (Forster & Forster, 2003) (Exp. 1) or Presentation® software (Version 0.70, www.neurobs.com) (Exp. 2) and it was conducted on an Intel Pentium® 4 CPU 3.06GHz (2 CPUs) computer running on the operating system Windows XP Professional 5.1 with a Belinea 17 Zoll TFT-Monitor. Spoken responses were recorded with a Sennheisser

PC131 headset microphone. Voice key triggers were manually corrected using the Checkvocal tool for DMDX (Protopapas, 2007).

5.2.3 Results

Responses were coded as erroneous and excluded from the analysis for the following reasons: the subject gave a response before the voice key trigger was activated or after the cue had disappeared, when a distractor was named in the experimental condition or the picture was named in the filler condition. Also incorrect picture designations (e.g. responding "stick" for picture "flute"), stutterings (e.g. "sti .. uh .. flute") and missed answers were excluded from the analysis.

For the outliers, the same exclusion criteria were used as in Chapter 5.1, i.e. all reaction times shorter than 100 ms or longer than 1800 ms were removed.

The data were analysed with linear mixed effect models using the package *lme4* (Bates et al., 2015) in *R* (Version 3.0.2) (R Core Team, 2014), with the random factor participant and the fixed factors cue, condition and their interaction. The independent variable *reaction time* was logarithmized.

Post hoc tests for the interaction term were performed with Least Square Means.

Exp.1: SOA Variation

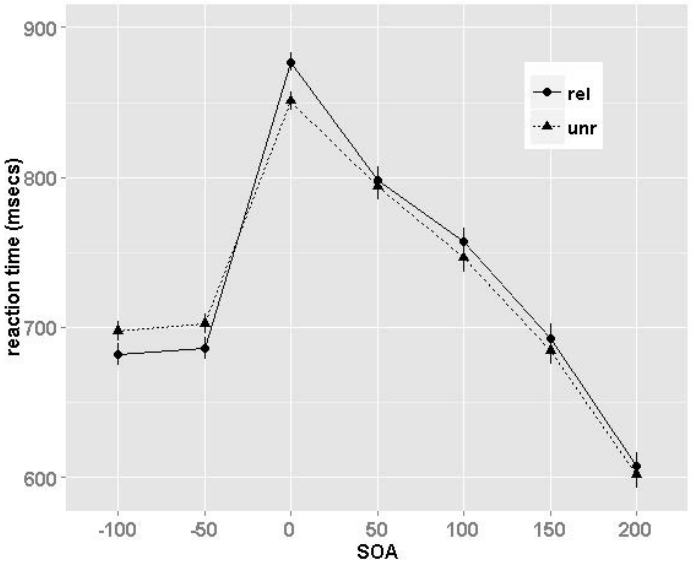
Overall, the stimulus-onset asynchrony *SOA* had a significant effect on the reaction times ($\chi^2(3) = 588.7718, p < .0001$) but the relatedness of target picture and distractor (*condition*) did not ($\chi^2(2) = 1.2816, p = .26$). For the mean reaction times across condition and SOA, see Table and Figure 5.6.

Reaction times were affected by the combined effect of *SOA* and *condition* ($\chi^2(4) = 4.7376, p = .03$).

The picture naming latencies (reaction times; RTs) were increased in the context of a related compared to an unrelated distractor, when the target picture and the distractor were presented simultaneously (SOA = 0 ms, $b = -0.029, p < .05$). If the word was presented *after* the picture, the reaction time difference between the related and the unrelated condition was not statistically significant (SOA = 50 ms, $b = -.031, p = 1$; SOA = 100 ms, $b = -.015, p = .99$; SOA = 150 ms, $b = -.009, p = 1$; SOA = 200 ms, $b = -.009, p = 1$)). If the word was presented *before* the picture, in the presence of a related distractor picture naming reaction times were slightly decreased, but the difference was not significant (SOA = -100 ms, $b = .031, p = .31$, SOA = -50 ms, $b = .029, p = .57$).

Figure 5.6: Mean reaction times across condition and stimulus-onset asynchrony (SOA)

	related		unrelated		
SOA	RT	SD	RT	SD	diff
-100	682	(189)	697	(159)	-15 .
-50	686	(170)	702	(147)	-16 .
0	877	(209)	851	(201)	26 *
+50	798	(202)	794	(207)	4 .
+100	757	(237)	746	(238)	11 .
+150	693	(227)	685	(221)	8 .
+200	607	(240)	602	(224)	5 .

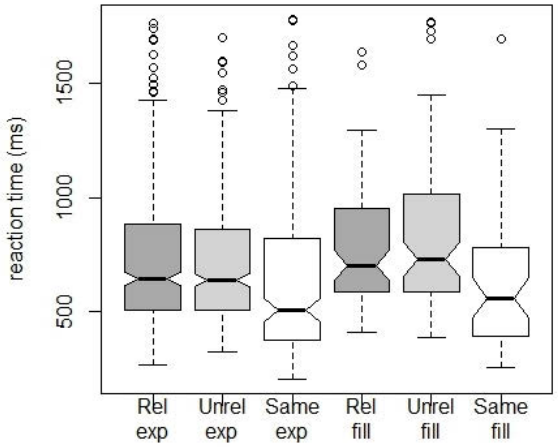


* = p ≤ .05; . = p > .05 (not significant)
Stimulus-onset asynchrony (SOA), mean reaction times (RTs), and the RT difference between the related and the unrelated condition (diff) are displayed in milliseconds. Standard deviation (SD) is given in brackets. As customary, negative SOAs designate the pre-exposure of the distractor, positive SOAs its post-exposure. The figure is provided with the standard error of the mean (SEM).

Exp.2: Delayed Naming

Overall, *condition* had a significant effect on the reaction times ($\chi^2(3) = 150.19, p < .0001$) and so did *cue* ($\chi^2(2) = 10.76, p = .01$). Reaction times were not significantly affected by the combined effect of *cue* and *condition* ($\chi^2(4) = 3.82, p = .14$). Post hoc tests revealed that during picture naming, reaction times were significantly increased for the *related* condition compared to the *same* condition ($b = 0.22, t(7) = 10.233, p < .0001$). Reaction times were also increased for the *unrelated* condition compared to the *same* condition($b = 0.20, t(7) = 9.047, p < .0001$). Reaction times for the *related* and the *unrelated* condition did not differ significantly ($b = 0.025, t(7) = 1.428, p = .71$).

Figure 5.7: Exp. 2: delayed naming PWI - Mean reaction times across condition)



condition			
exp ("name picture")			
	RT	SD	error
related	721	(286)	0.2%
unrelated	695	(263)	0.2%
same	615	(336)	0.0%
filler ("name distractor")			
	RT	SD	error
related	729	(270)	0.2%
unrelated	835	(322)	0.3%
same	632	(326)	0.1%

Mean reaction times (RTs) are given in milliseconds with standard deviation (SD; in brackets) and error rates.

5.2.4 Discussion

In the first experiment, picture naming latencies were increased in the presence of a related distractor word, but only when picture and word were presented simultaneously. The interference effect was not significant at SOAs as short as +50 ms, i.e. with the word presented shortly after the picture. If the related word was displayed before the picture, it tended to facilitate naming, but the impact was not significant.

In the second, delayed naming paradigm, naming latencies for the related and the unrelated condition did not differ significantly.

Hence, for delayed naming, both behavioural experiments showed no significant semantic interference effect, in line with most studies (Mädebach et al., 2011; Piai et al., 2011). The findings indicate that semantic interference is unlikely to occur at the response stage.

In the identical condition of the delayed naming paradigm, the picture was presented together with its name, which led to decreased naming latencies. The facilitation effect in this condition reflects the fact that attentional demands were strongly decreased for two reasons: Because the picture and the word were identical, only one lexical item had to be processed and memorized. In addition, also the source of the word, i.e. whether it originated from the picture or the word, could be neglected.

In conclusion, in the delayed version of the Picture-Word Interference task, a Stroop effect is present, but an interference effect is not.

5.3 Comparison Stroop versus PWI

In the previous section, two temporal variations of the Numerical Stroop paradigm (NSP) and the Picture-Word Interference (PWI) task were investigated behaviourally. The NSP was designed to induce and capture interference in the number core system. Conflicts in the object core system, on the other hand, were explored with the PWI. We are now able to compare the results.

In the NSP, incongruent numbers were expected to come into conflict with the counting performance whereas in the PWI, semantically related words were supposed to interfere with picture naming.

The results show a striking resemblance for the interference effect in both paradigms. Indeed, the task-irrelevant distractor cannot be ignored and it interferes with the participants' task performance, but only if the distractor is presented simultaneously with the target. In the delayed variations of the paradigms, an interference effect is not observed. The results indicate that the conflict does not occur at the response stage.

Naming latencies for the identical conditions are strongly decreased in both paradigms. The facilitation may, again, be explained with the fact that attentional demands were strongly decreased in this condition.

In conclusion, in both immediate versions of the Numerical Stroop task and the Picture-Word Interference task, an interference effect as well as a Stroop effect are observed.

However, in the delayed version of the Numerical Stroop task and the Picture-Word Interference task, the interference effect is not observed, but the Stroop effect is still present.

Consequently, the results indicate that interference in the numerical core system and the object core system can be explained with a single cognitive process underlying both tasks.

Chapter 6

fMRI Experiments

The previous chapter portrays that, behaviourally, the conflicts in the Numerical Stroop and the Picture-Word Interference task show a striking resemblance. The interference effect is observed when the task-irrelevant distractor is presented simultaneously with the target, but it disappears whenever the presentation of the distractor is delayed. However, with only one behavioural measure, the source of the interference effect cannot be located directly, instead, it must be deduced from the response latencies. As a consequence, I'm using a fMRI experiment, which allows me to separately model the BOLD response associated with retrieval and response selection.

In Chapter 6.1 I will present an fMRI investigation of the Numerical Stroop task, in Chapter 6.3 of the Picture-Word Interference task and in Chapter 6.5 a combined analysis of the two.

To be able to pinpoint the locus of the interference effect, a functional MR imaging experiment was designed to investigate the two critical time periods in a delayed paradigm. The trial sequence is outlined in Figure 6.1. As illustrated, the BOLD signal is modelled, first, for the retrieval phase, in which the stimulus (picture or number) is retrieved, encoded and memorized and second, for the response phase, in which the correct answer is selected and given orally. For each time period in the trial, different brain areas are supposed to reflect an increased demand, elicited either by the retrieval or by the response conflict.

However, we have to keep in mind that, in the present task, the participant is confronted with various challenges: During the retrieval phase the subjects had to chose and select the target (name/quantity) and the distractor word from a pool of responses. Because the participants did not know whether they had to respond with the target or the distractor, they did not only have to encode and memorize both, but they also had to remember their respective source. During the response phase, the cue indicated whether the subject had to respond with the prepared target or distractor word. As mentioned previously, in the congruent (NSP) and the same condition (PWI) the target and the distractor referred to the same lexeme. Therefore this response could already be prepared. In these conditions, the colour of cue was irrelevant.

6.0.1 Hypotheses Numerical Stroop

During the **counting phase** a higher cognitive demand is assumed to be reflected by increased brain activity in areas which are reported to be involved in numerical processing: These are mainly parietal regions, more particularly the bilateral horizontal segment of the intraparietal sulcus (hIPS) (Dehaene et al., 2003, 2004; Dehaene, 2011; Eger et al., 2003; Piazza & Dehaene, 2008; Piazza et al., 2007), possibly with a right hemispheric dominance (Chassy & Grodd, 2012).

During the **response phase**, the counting procedure is supposed to be terminated. Conflicts are assumed to be reflected by increased brain activity in brain areas which are reported to be key regions for supervisory attentional control. Such areas are mostly dominant in the right hemisphere (Cieslik et al., 2015) and include the inferior frontal junction (Brass et al., 2005; Cieslik et al., 2015; Derrfuss et al., 2004, 2005; Kim et al., 2012; Levy & Wagner, 2011; Sundermann & Pfleiderer, 2012). Also anterior cingulate cortex (ACC) activation is supposed to reflect response conflicts (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, 2007; Cieslik et al., 2015; Gasquoine, 2013; Levy & Wagner, 2011; Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008; Shenhav, Straccia, Cohen, & Botvinick, 2014; Sundermann & Pfleiderer, 2012).

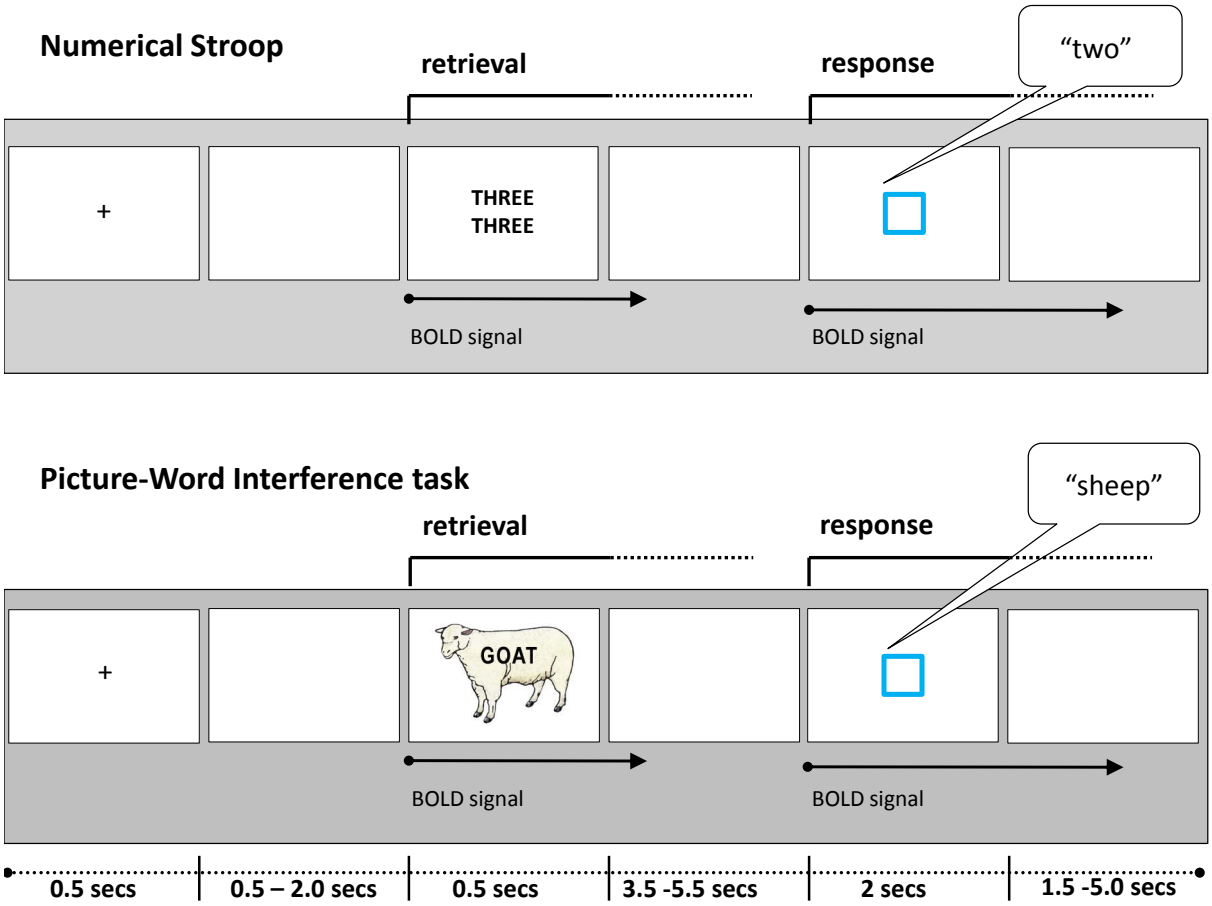


Figure 6.1: Schematic trial sequence for the functional MR imaging experiments. Example for the Numerical Stroop task (top) and the Picture-Word Interference task (bottom). The duration of all blank screens was varied (jittered). The temporal design was identical for both paradigms. The total trial duration always added up to 12 seconds.

The **numerical distance effect** is reported to manifest in parietal areas, in particular in the inferior and superior parietal lobe (Bulthé et al., 2014; Kaufmann et al., 2005; Fulbright et al., 2003; Piazza et al., 2007; Pinel et al., 2001). In addition, responsiveness to numerical distance was observed in the bilateral anterior insula (Kaufmann et al., 2005), the inferior and superior frontal gyrus (Bulthé et al., 2014; Kaufmann et al., 2005; Piazza et al., 2007) and the anterior and posterior cingulate gyrus (Kaufmann et al., 2005; Pinel et al., 2001).

6.0.2 Hypotheses Picture-Word Interference

Brain areas which respond to an intensified demand elicited by **lexical retrieval** are reportedly dominant in the left hemisphere and include the left middle temporal gyrus (Maess et al., 2002; Friederici, 2012; Indefrey & Levelt, 2004; Indefrey, 2011) and the left middle frontal gyrus, extending to the inferior frontal gyrus (Price, 2012).

During the **response phase**, the lexical retrieval is supposed to be completed successfully. Accordingly, the response conflict is expected to manifest in the same areas as described for the Stroop task (see the previous paragraph 6.0.1). According to a review on speech production by Price (2012) an anterior zone in the anterior cingulate cortex is associated with response suppression in overt speech.

6.1 Numerical Stroop

6.1.1 Methods

Participants

22 students of the Humboldt-Universität zu Berlin participated in the experiment (10 women). They were recruited using the subject database PESA. Their mean age was 25.45 years (SD=4.47, range=19-37). All participants reported to be right-handed and native speakers of German. None of the participants suffered from psychiatric or neurological disorders or had ever suffered a head injury.

One of the participants failed to comply with the experimental conditions. For another participant, recordings were not obtained due to a technical error. The data from these participants were excluded from the analysis conducted of the final sample of 20 subjects (9 women), with a mean age of 25.7 years (SD=4.59, range=19-37).

The study was approved by the Charité Berlin Ethics Committee. Participants gave informed consent before their participation and were paid 25 Euro.

6.1.2 Material

The number word and the quantity of the word(s) could either be congruent or incongruent. In the neutral condition, common nouns were counted. For the congruent and the incongruent condition, German number words, ranging from 'one' to 'six', were used. For the neutral condition, the German nouns 'Mann' (man), 'Frau' (woman), 'Haus' (house) and 'Tier' (animal) were presented.

The frequency of the number words and the common nouns was matched (see section 5.1 'Behavioural NSP', p. 45).

To increase the number of observations for the congruent condition, the congruent items were presented three times. In total, 128 experimental items were used (18 congruent, 30 incongruent, 24 neutral). As filler trials, 9 congruent, 21 incongruent and 26 neutral items (43%) were presented with a red cue. In addition, 21 to 41 null trials were added.

The words were capitalized. The experiment was conducted in German.

In the final fMRI analysis, to adjust the number of observations in the incongruent and the neutral condition to match the number of observations in the congruent condition (i.e. 18), the quantity of the incongruent and neutral target-distractor combinations were reduced to 20 observations ($= 4 \times 5$) each. The items were chosen at random.

Procedure

Two runs were conducted in a single session. The Picture-Word Interference (PWI) task was always conducted first, followed by the Numerical Stroop task. The PWI will be described and discussed in Chapter 6.3. In between the runs, the participants were allowed to rest, but they did not leave the scanner.

The participants were instructed to memorize the number and the quantity and to withhold the response until a cue was shown. The colour of the cue indicated the response to be given. The blue cue indicated to respond with the quantity, the red cue indicated to respond with the word.

To be able to uniquely estimate the BOLD response, in fast event-related functional MR imaging studies it is suggested to add randomized, variable intervals between stimuli. A range of varied, i.e. jittered, intervals between stimuli is suggested to improve the accuracy of the measurement (Zarahn, Aguirre, & D'Esposito, 1997; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Accordingly, six temporal variations were used, adding up to a total trial duration of twelve seconds (see Appendix, Table A.3). First, a fixation cross was presented for 0.5 seconds, then a blank screen was presented for 0.5 to 2 seconds in steps of 0.5 secs. Then the stimulus was presented for 0.5 seconds. Subsequently, a blank screen was presented for 3.5 to 5.5 seconds. Then the cue was shown for 2 seconds. The last blank screen was presented for 1.5 to 5 seconds.

Also the length of the null trials varied from 2 to 6 seconds, they were randomized and optimized with Optseq (`https://surfer.nmr.mgh.harvard.edu/optseq/`).

Before fMRI scanning commenced, participants performed a practice trial outside the scanner with stimuli which were not part of the actual experiment.

6.1.3 Data Acquisition and Analysis

Structural and functional data were acquired on a Siemens 1.5 T MR scanner equipped with a circular polarized Head Coil (Siemens Sonata, Erlangen, Germany). Earplugs were provided to attenuate background noise, a vacuum head cushion was used to immobilize the participants' heads, and stimuli were presented on a head-mounted display attached to the headcoil.

Participants' responses were recorded with a FOMRI-III Noise Cancelling Microphone by Opto-Acoustics.

T1-weighted structural images were collected (spatial resolution 1x1x1 mm, TR=12.24 ms, TE=3.56 ms, flip angle=23 deg, 256x224x176 matrix) (Deichmann, 2005). T2*-weighted single-shot gradient echo planar imaging data were acquired aligned to the AC-PC plane to cover the temporal lobe (resolution 3x3x3 mm, TR = 2000 ms, TE = 40 ms, flip angle = 90 deg, FOV 192 mm, interleaved).

Functional images were collected in two runs in a single session (PWI comprising 1060 volumes; Numerical Stroop comprising 770 volumes). The PWI will be described and discussed in Chapter 6.3.

The experiment was programmed with Presentation software (Version 0.70, www.neurobs.com)

Preprocessing

Off-line data analysis was performed using SPM8 (*Statistical Parametric Mapping*, 2009).

The first six images were discarded to eliminate magnetic saturation effects.

After slice time correction, all volumes were unwarped and realigned to the first volume in order to correct for between-scan movements and to remove signals correlated with head motion. The anatomical data set was coregistered with the mean T2* image, and T1-weighted images were segmented into grey matter, white matter, and cerebrospinal fluid. The gray matter of the coregistered structural image was spatially normalized to the standard template provided by the Montreal Neurological Institute (MNI template) using an automated spatial transformation. The resulting transformation matrix was subsequently applied to the T2* data, and a resampling to a resolution of $3 \times 3 \times 3$ *mm* voxel size was performed. Last, spatial smoothing was performed with a 8 mm full-width at half-maximum (FWHM) Gaussian kernel.

Data of five participants showed occasionally rapid head movements. These image volumes were repaired by applying a noise filter (ArtRepair, `http://cibsr.stanford.edu/tools/ArtRepair/ArtRepair.htm`), that is, replaced by interpolation of neighbouring volumes ($< 5\%$ of volumes for each subject).

Subject Level fMRI Analysis

The preprocessed functional volumes were submitted to a fixed-effects analysis, using the general linear model (GLM) at each voxel.

Each stimulus onset and each cue onset was modelled as an event, and was convolved with a canonical hemodynamic response function, thus providing regressors for the linear model. The baseline contrasts, the filler contrasts and the contrasts of interest were computed at the first level analysis. The final model included six experimental task regressors, six filler task regressors, an error term, the null events and six motion parameters.

The six contrasts of interest in the experimental condition were (1) stimulus onset, i.e. counting, retrieving and memorizing the quantity and the number word, the distractor word is either (a) incongruent (b) neutral (i.e. not a number) or (c) congruent and (2) response onset , i.e. choosing and articulating the prepared quantity in the context of an (a) incongruent (b) neutral or (c) congruent number word.

The filler contrasts were modelled in the GLM on subject level, but they were not analysed in the second level analysis. Also erroneous trials were modelled with a separate regressor.

The contrast images for each of the six conditions against implicit baseline were then entered into the second-level analysis, i.e. random-effects analysis (Gläscher & Gitelman, 2008) to enable inferences at group level.

Group Level Analysis

The second level analysis was conducted with a flexible factorial design (commonly know as random effects in SPM) on the corresponding contrast images as suggested by Gläscher and Gitelman (2008). Again, filler trials were included in the GLM on subject level, but not analysed in the second level analysis.

Percent Signal Change Also the direction (activation and deactivation) and the amplitude of the signal change, reflected by the β-weights was explored for some regions of interest, as calculated by Rfxplot (Gläscher, 2009). According to Gläscher (2009) Percent Signal Change is computed as

$PSC = \frac{\beta_{task} \times max(HRF) \times 100}{\beta_{constant}}$

where β_{task} refers to the parameter estimate of the effect of interest, $max(HRF)$ is the maximum of the a single event of the current duration convolved with the current basis function, and $\beta_{constant}$ the parameter estimate of the current session constant.

Thresholding Statistical significance was set to $p < .05$, corrected with a cluster-size based correction for multiple comparisons: By using a combination of probability thresholding and cluster thresholding the power of the statistical test is maximized while holding the likelihood of false positives to a minimum. The Alphasim program, as implemented in Resting-State fMRI Data Analysis Toolkit V1.5 (Song et al., 2011) was used to determine the cluster threshold. The program is provided with the number of voxels in the group map, the spatial correlation of voxels, and the voxelwise threshold (in this study, $t > 3.17$, $p < .001$). A series of Monte Carlo simulations (10,000 iterations) was then carried out to determine the frequency of each conforming cluster size produced purely by chance. From this frequency distribution, the cluster size (100 voxel) that occurs $< 1\%$ of the time by chance was selected, to give a threshold of $p < .05$ (corrected).

Labelling Brain areas were labelled with the Anatomy toolbox (Eickhoff et al., 2005, 2007) and additionally with the Talairach demon (Lancaster et al., 2000) after being transformed from MNI coordinates to Talairach coordinates using mni2tal algorithm (Lancaster et al., 2000) implemented in Ginger Ale (brainmap.org, 2015).

For the figures, the resulting T-maps were projected to the cortical T1 template provided by the software 'FIVE' (Schultz & McLaren, 2014) or 'Mricron' (Rorden & Brett, 2000).

Conjunction The present study used the *MS/CN* conjunction as defined by Nichols, Brett, Andersson, Wager, and Poline (2005) and as implemented in SPM8 (*Statistical Parametric Mapping*, 2009). Different models were set up for the Numerical Stroop task and the Picture-Word Interference task, therefore a conjunction across paradigms could not be performed for the comparison. Instead, as suggested by Donald MacLaren by personal advice (MacLaren, 2014) and in the SPM jiscmail forum (MacLaren, 2015), implicit masking was performed. To do so, each map was thresholded, corrected for multiple comparisons, converted to a binary value, then the two images were added together with ImCalc (*Statistical Parametric Mapping*, 2009).

Numerical Distance

For modelling the task difficulty, a separate model was set up. Here, parametric modulation regressors for the incongruent conditions were added.

Changes in the BOLD response were assessed using linear and quadratic combinations of the estimated GLM parameters (beta values) and contained in the individual contrast images.

The corresponding eight regressors for the filler condition were also included in the design matrix, as well as an error and six realignment regressors. Regressors were convolved with the canonical hemodynamic response function. Contrasts were generated for both the first and the second level analysis.

For the fMRI group analyses, all images of all subjects were analysed in one design matrix, generating a random-effects model, allowing inference to the general population. The cluster-corrected significance threshold of $p < .05$, with a minimum cluster extent of $k > 75$ was obtained with AlphaSim (REST toolbox, Song et al., 2011).

6.1.4 Behavioural Results

The responses of the subjects were recorded with a FOMRI-III Noise Cancelling Microphone by Opto-Acoustics. To reduce scanner noise, the resulting wav-files were processed with a positive low pass filter of 700 Hz and positive smoothing filter of 50 Hz in Praat (Boersma & Weenink, 2012). The reaction time at the response onset was determined with Checkvocal (Protopapas, 2007). The answers of four subjects could not be processed in Checkvocal due to technical reasons. Therefore, reaction times of 15 subjects were analysed. Error rates, by contrast, were analysed for all participants.

Error and Outlier

Items were coded as inaccurate and excluded from analysis for the following reasons: missing or delayed response (later than 2 seconds after cue presentation), self-corrections, reading the number word in the experimental condition or the quantity of number words in the filler condition, wrong quantity/number, noisy recording. 2.9% of the data were erroneous and therefore excluded from further analysis. In addition, all reaction times larger than 1800 ms and shorter than 100 ms were removed (3.7%).

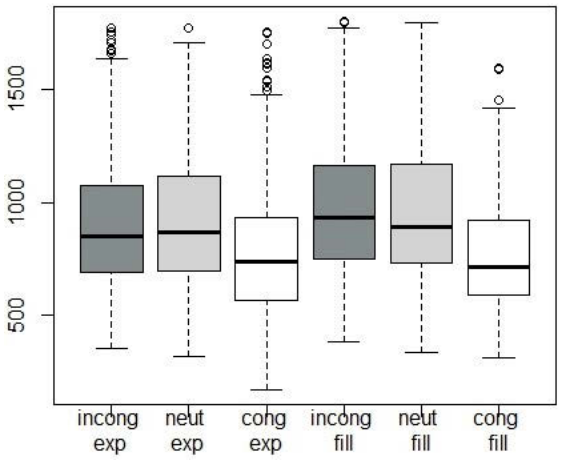
Pearson's χ^2 tests using the software *R* (Version 3.0.2) (R Core Team, 2014) for the experimental trials revealed that the error rates did not differ significantly across conditions, neither overall ($\chi^2(5) = 6.042, p = .30$) nor for the experimental counting trials ($\chi^2(2) = 5.710, p = .06$).

Analysis

The data were analysed with LMERs fit by maximum likelihood, using the software *R* (Version 3.0.2) (R Core Team, 2014) with the random factor *participant* and the fixed factors *cue*, *condition* and their *interaction*. To convert the independent variable *reaction time* to a normal distribution, it was logarithmized. Post hoc tests for the interaction term were performed with Least Square Means. For the Numerical Stroop task, in addition, also the *absolute distance* was included in the analysis.

Results

Figure 6.2: Numerical Stroop task: mean response latencies



condition			
experimental ("count")			
	mean(ms)	SD	error
incongruent	914	(303)	3.6%
neutral	926	(301)	4.4%
congruent	806	(309)	1.1%
filler ("read")			
incongruent	980	(307)	1.5%
neutral	955	(288)	3.3%
congruent	788	(294)	1.1%

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses. RTs were obtained during functional imaging. The overt responses were processed with a positive low pass filter to reduce scanner noise and onsets were determined with Checkvocal (Protopapas, 2007).

The different *conditions* had a significant influence on the naming latencies ($\chi^2(2) = 41.49, p < .0001$). For the mean reaction times see Figure and Table 6.2. Over all, reading the number word (mean naming latency: 943 ms) took longer than naming the quantity (890 ms) ($\chi^2(3) = 7.88, p < .001$).

And also the combined impact of the *conditions* and the *cue* did have a significant impact on the reaction times ($\chi^2(4) = 6.23, p < .05$).

Post hoc test revealed that responses were slowed for *incongruent* number words compared to congruent number words, both, when responding with the quantity ($b = 0.14, t(22) = 6.101, p < .0001$) and for reading the number ($b = 0.23, t(22) = 7.042, p < .0001$).

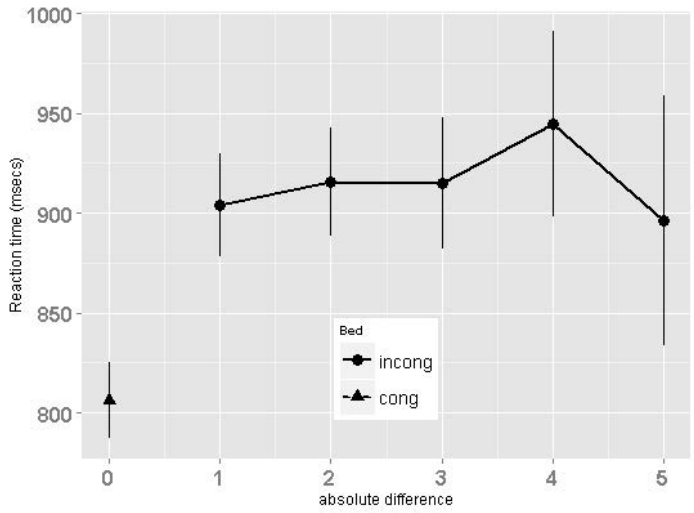
Reaction times were also increased in the *neutral* condition compared to the congruent condition when responding with the quantity ($b = 0.15, t(22) = 6.360, p < .0001$) and for reading the distractor ($b = 0.21, t(22) = 6.634, p < .0001$).

The responses for the common noun distractors (neutral condition) and the incongruent number words did not differ, neither for the counting trials ($b = -0.011, t(22) = -0.513, p = .99$) nor for reading the distractor word ($b = 0.019, t(22) = 0.788, p = .97$).

Hence, the response times for the incongruent and the neutral condition did not differ, but they are decreased for the congruent condition. These findings are in line with the results from previous delayed naming experiment (see Chapter 5.1.3 *Delayed naming NSP*, p. 49 ff.).

The absolute distance between target and distractor did not have significant influence on the reaction time ($\chi^2(5) = .006, p = .94$), hence, a behavioural numerical distance effect was not observed.

Figure 6.3: Numerical Stroop mean reaction times (RTs) for the absolute distance between target and distractor



experiment ("count")		
dist	RT	SD
0 (= congruent)	806	(309)
1	904	(298)
2	916	(286)
3	915	(306)
4	944	(346)
5	896	(319)

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses. The figure is provided with the standard error of the mean (SEM). All RT onsets were determined with Checkvocal (Protopapas, 2007).

6.1.5 Functional Imaging Results

First, I aimed to identify the brain network, in which activation is modulated by the counting procedure (*Task*) and the naming procedure (*Response*).

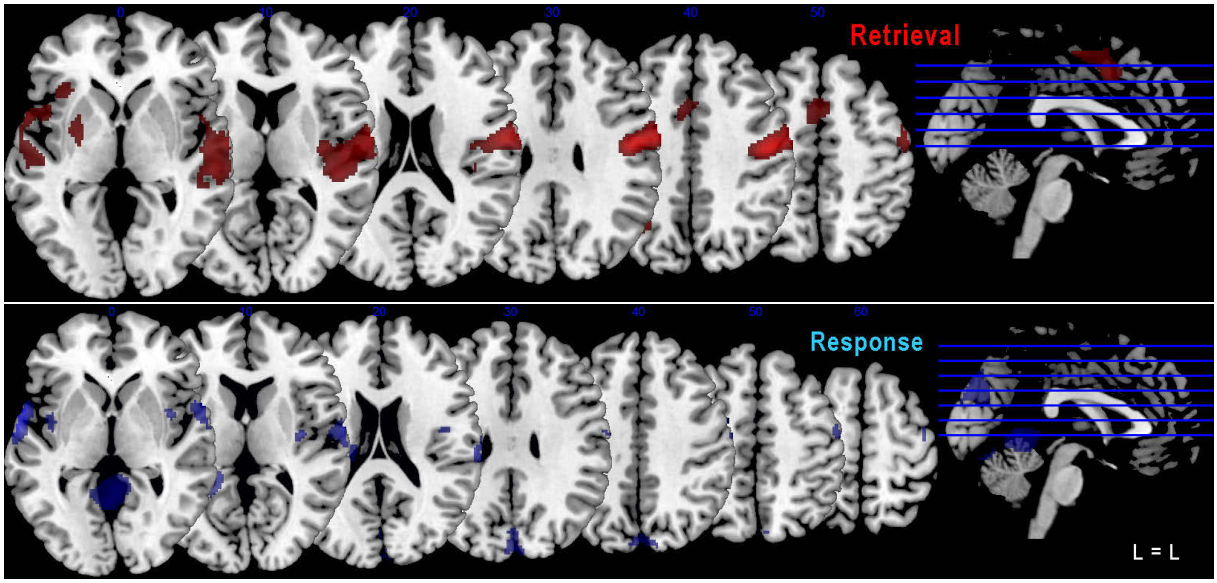
General task- and response-related Brain Network While the participants performed the counting task (task> implicit baseline), enhanced activity in bilateral postcentral gyri and the SMA was observed (see Table 6.1 and Figure 6.4). In addition, the left superior and inferior parietal cortex, including the hIPS, the left insula and lentiform nucleus are active.

Also during the response phase of the task, a large frontal, temporal, occipital and subcortical network is found active, comprising the bilateral superior temporal gyri, right precentral gyrus and insula, right precuneus and cuneus and, finally, cerebellar, thalamic and parahippocampal areas.

During the task *and* the response phase, the transverse temporal region, in particular Heschl's gyrus (BA 42) is found active in both hemispheres, with a left hemispheric dominance (see Appendix, Table A.4). Heschl's gyri, which are part of the STG, are known to be involved in the auditory processing of speech and nonspeech sounds (Price, 2012). Most likely, the activity in Heschl's gyri was caused by the noisy surrounding in the scanner, albeit its left hemispheric dominance may also indicate the processing of intelligible speech (Friederici, 2012; Price, 2012).

Presumably, the activity in those frontal areas, including precentral gyrus, SMA and insula, as well as cerebellar and thalamic regions, support the timing, control and execution of muscular movements in overt articulation (Price, 2012). Early[1], during the counting procedure, it is likely, that the activity was caused by internal rehearsal or a 'phonological loop' (Baddeley, 2003) and late, due to the overt response.

Figure 6.4: Numerical Stroop: General task- and response-related Brain Network.



Whole-brain results were obtained post stimulus onset ('retrieval phase' = red) and post cue onset ('response phase' = blue). MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < .05$, with a minimum cluster extend of $k > 100$ derived with $p < .001$ and displayed with neurological orientation (left = left). Figure created with Mricron (Rorden & Brett, 2000). For the corresponding coordinates, see Table 6.1

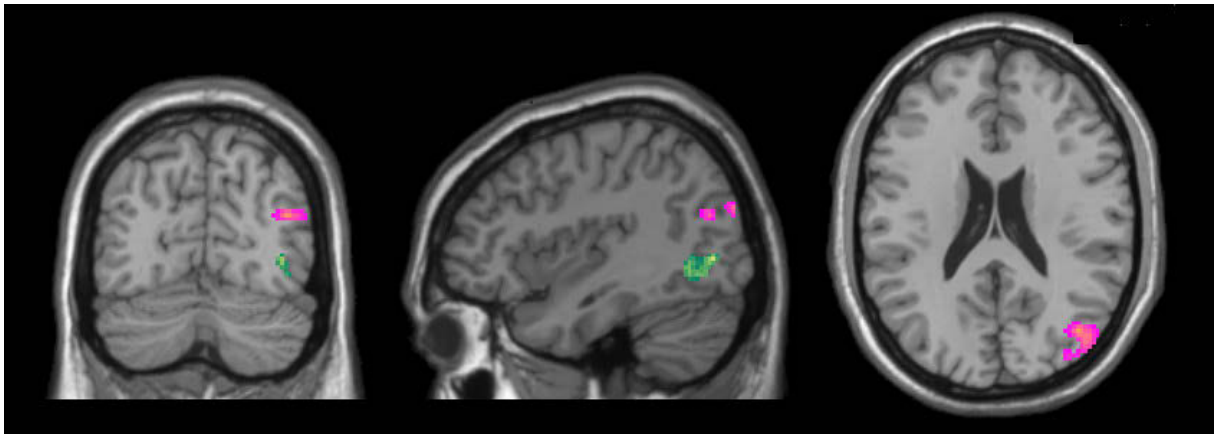
[1] With *early*, I designate the counting phase; with *late* I refer to the response phase.

Table 6.1: Neural network for task and response in the Numerical Stroop task.

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Task > base					
Left postcentral gyrus (4/42)	-44	-16	34	10.54	2913
	-56	-8	28	9.45	
	-60	-12	8	6.63	
Right postcentral gyrus (4/43)	48	-12	36	10.03	2956
	62	-6	32	8.22	
	66	-4	12	6.53	
SMA (6/32)	0	14	46	5.03	496
and dorsal anterior cingulate area (dACC)	-2	-2	58	4.81	
	0	8	56	4.23	
Left insula (13)	-34	24	4	4.67	140
Left superior parietal lobe / AG (39)	-32	-60	44	4.40	305
Left inferior parietal lobe (hIP3) (40)	-46	-50	52	4.40	
	-52	-44	46	3.68	
Left lentiform nucleus (pallidum)	-26	-6	-4	4.29	156
Response > base					
Left superior temporal gyrus (22, 42)	-62	0	2	7.79	1734
	-66	-20	14	6.51	
	-66	-12	8	6.46	
Right superior temporal and	66	-10	10	5.95	509
supramarginal gyrus (22,40)	60	10	-4	5.71	
	66	-22	18	4.67	
Right precentral gyrus (4, 6)	50	-8	56	5.32	154
	64	-10	36	3.96	
	62	-2	36	3.65	
cerebellum	-12	-60	-12	5.01	1167
	2	-52	0	4.93	
	20	-62	-16	3.94	
Right precuneus and cuneus (18,19)	8	-80	46	4.80	396
	8	-86	38	4.55	
	2	-90	28	4.44	
Right superior temporal gyrus (38)	40	4	-16	4.25	135
	40	4	-2	4.14	
Right insula (13)	36	-10	12	4.18	106
	44	-8	18	4.11	
Left thalamus and	-18	-30	16	4.09	137
parahippocampal gyrus (30)	-20	-42	10	3.99	
	-20	-22	20	3.78	

Results were obtained post stimulus onset ('task') and post cue onset ('response'). MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < .05$, with a minimum cluster extend of $k > 100$ derived with $p < .001$. Labelling was provided by the Anatomy toolbox (Eickhoff et al., 2005), Brodmann areas in parentheses. For the corresponding images, see Fig. 6.4.

Figure 6.5: Numerical Stroop task: Interference effect and reverse Stroop effect



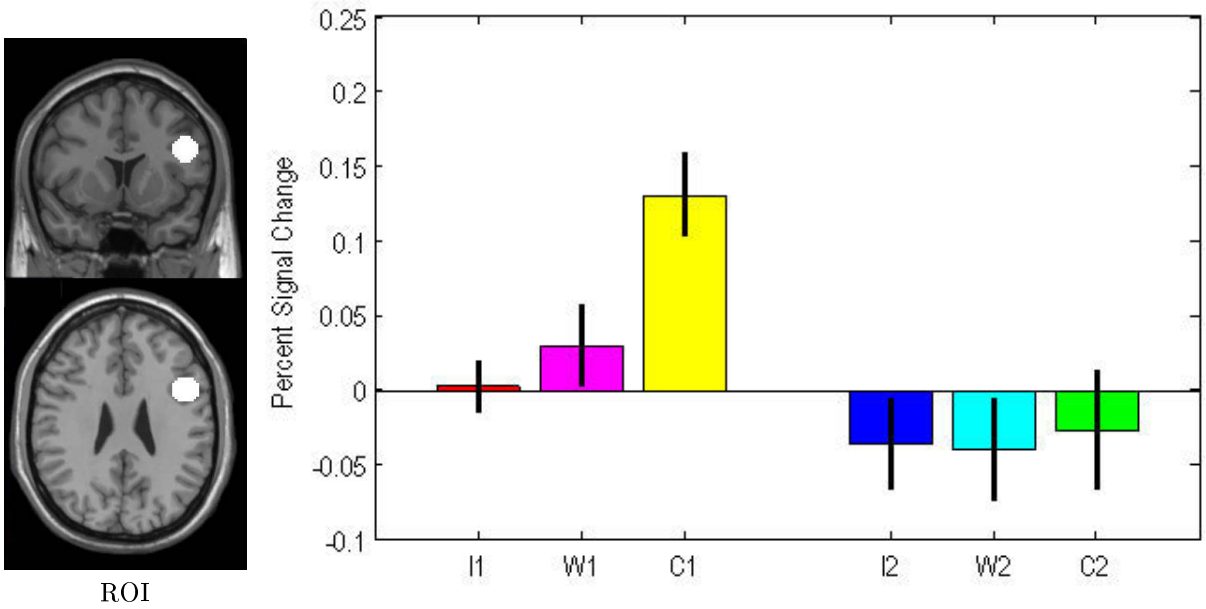
Maps of brain regions in which the BOLD signal was modulated by the interference effect (green) or the reverse Stroop effect (pink). MNI coordinates derived from T-maps with T > 3.17, at a cluster-corrected significance threshold of p < .05, with a minimum cluster extend of k > 100 derived with p <.001. T-maps were projected on a T1 template provided by FIVE (Schultz & McLaren, 2014) with neurological orientation (left = left). For the coordinates, see Table 6.2.

Table 6.2: NSP fMRI results: Counting or retrieval phase

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Interference (incong>neutral)					
Right inferior temporal and lingual gyrus (19)	42	-68	-8	4.52	163
	32	-62	-1	4.29	
	34	-71	-2	4.22	
Reverse interference (neutral>incong)					
	n.s.				
Stroop effect (incong>cong)					
	n.s.				
Reverse Stroop (cong>incong)					
Right inferior frontal gyrus (p. opercularis) and	60	18	16	4.95	100
inferior frontal junction (44)	52	4	10	4.00	
Right middle occipital gyrus and	40	-72	22	4.23	173
inferior parietal cortex (PGp) or	42	-82	26	4.01	
'temporo-occipito-parietal junction'	34	-84	24	3.88	

Whole-brain analysis results for the *retrieval phase* of the Numerical Stroop task. Results were obtained post stimulus onset. MNI coordinates derived from T-maps with T > 3.17, at a cluster-corrected significance threshold of p < .05, with a minimum cluster extend of k > 100 derived with p <.001. Labelling was provided by Talairach Daemon (Lancaster et al., 2000) and the Anatomy toolbox (Eickhoff et al., 2005). For the corresponding image, see Fig. 6.5.

Figure 6.6: Numerical Stroop task: Percent Signal change of beta weights within right IFJ



Inferior frontal junction ROI defined with rfxplot, as an 8 mm sphere at MNI coordinates [+46, +6, +36] (Brass et al., 2005), resulting in 513 voxel, which were included in the analysis. I=Incongruent, W=word/neutral, C=congruent / 1=Retrieval, 2=Response.

Interference and Stroop For the *Interference contrast* the incongruent condition was compared to the neutral condition. In particular, the counting of number words which were incongruent with the quantity (e.g. 'four four four'), was compared to the counting of common nouns (e.g. 'man man man'). For the interference effect during the counting phase, the BOLD signal was increased in the right inferior temporal gyrus (see Figure 6.5 and Table 6.2, top). Its most anterior superior cluster was located in the right lingual gyrus, extending posterior inferior along the fusiform gyrus to the occipital gyrus (BA 19).

No significant activation clusters were found for the *reverse interference effect* (neutral > incongruent condition).

For the *Stroop effect*, the incongruent condition was contrasted with the congruent condition. In the congruent condition the quantity and the number word were identical (e.g. 'four four four four'). The Stroop effect was not significantly correlated with the BOLD signal.

However, for the *reverse Stroop effect* (congruent > incongruent condition), changes in the BOLD signal correlated with two widely separated clusters in the right hemisphere. One of these clusters was located on the junction of the right occipito-parietal cortex (see Figure 6.5 and Table 6.2, bottom), which is also referred to as temporoparietal junction (TPJ). The anterior part of the frontal cluster was based in the pars opercularis (BA 44) and encompassing the inferior frontal junction (IFJ) (Brass et al., 2005). To further illustrate the involvement of the right IFJ, it was measured, within a predefined ROI for the IFJ centred at [+46, +6, +36] as defined by Brass et al. (2005), how much the BOLD response deviated from the global signal for each condition (Gläscher, 2009); for the corresponding percent signal change graph see Figure 6.6.

In addition, it was investigated whether the incongruent and the neutral condition did rely on common neural substrates ('conflict > baseline' conjunction, i.e. incong + neutral > congruent) or whether joint activity could be detected for the opposite contrast ('congruent > conflict' conjunction), but both analyses did not yield significant results. Finally, a conjunction analysis on both numerical conditions (incongruent + congruent > neutral) did not detect joint activity.

6.2 Discussion

The aim of this investigation was to explore the neural representations of conflicts in the Numerical Stroop task during the counting phase and during the response phase.

Only during the counting phase, but not during the response phase (task network, Table 6.1), the

left inferior parietal cortex, or more particular the hIPS was found active (Dehaene et al., 2003, 2004; Dehaene, 2011; Eger et al., 2003; Piazza & Dehaene, 2008; Piazza et al., 2007). This result indicates that the hIPS was indeed involved in numerical processing or, more particular, in the counting process. The left-hemispheric dominance may reflect the fact that verbal stimulus material (number words and common nouns) was used (Arsalidou & Taylor, 2011).

Numerical Distance Contrary to expectations, activity in the hIPS was not modulated by numerical distance. Hence, the distance effect was neither detected behaviourally nor reflected by neural correlates. The numerical distance effect is typically observed in numerical comparison tasks, in which the participant has to compare and thus focus on the magnitude of two numbers. However, in the present Numerical Stroop task, admittedly the magnitude of the quantity or number word was irrelevant. For instance, in a study by Pinel et al. (2004), the numerical distance effect was only observed in the magnitude comparison task and not for physical size and luminance judgements of numbers.

Interference effect The interference effect was captured by comparing the incongruent to the neutral condition. As mentioned earlier, the interference effect was supposed to capture the conflict of the quantity with the incongruent number word as opposed to the influence of common nouns. For the interference effect, the BOLD signal was increased in a right hemispheric cluster in the inferior temporal gyrus (ITG) in Brodmann area 19, encompassing the lingual and fusiform gyrus.

There is some evidence that the ITG plays an important role in drawing attention to and detecting change in the overall context by masking its details: For instance, Fink et al. (1996) reported activity in the right lingual gyrus to reflect global as opposed to local attention. As stimulus material, so called Navon figures were used, that is, big letters which are composed of small letters. In the 'global' attention task, participants had to focus on the big letter, in the 'local' task, they had to pay attention to its small parts. Moreover, the right lingual gyrus seems to be involved in the detection of change. In a study by Pessoa and Ungerleider (2004) it was found active not only when a change was detected (change > no change), but also when a change was reported but had not occurred (false alarm > miss). The results are observed during the encoding phase of a task which is referred to as 'working memory' or goal-directed attention task by the authors. Finally – together with the right superior and inferior parietal lobe and precentral gyrus – the right lingual gyrus seems to be involved in spatial attention shifts as compared to holding attention (Yantis et al., 2002).

The findings indicate that the right lingual portion of the inferior temporal gyrus (BA 19) is involved in tasks where one has to 'see the forest for the trees', i.e. where attention is directed to the features *on top of the hierarchy*. More specifically, it reflects the effort to detect changes in the big picture by keeping away distractors or noise, and to maintain the information in short term memory, all of which was necessary to complete the present task successfully. It may thus reflect the higher cognitive demand of the specific task, however, it does not represent an increased demand in numerical processing.

Stroop effect For the Stroop effect, no significant brain activity was observed, neither during the retrieval phase nor during the response phase.

This finding is unexpected and it may also seem intriguing at first sight, because the incongruent condition was expected to be much more difficult to process, both, during the retrieval as well as the response phase:

As a reminder, during the retrieval phase of the *incongruent* condition, the quantity and the distractor referred to different numbers, which both had to be retrieved and stored during the counting phase. In the congruent condition, on the other hand, both numbers were identical and could therefore be merged into one response. Hence, during the response phase of the incongruent condition one of two responses had to be chosen, whereas in the congruent condition, the response was already prepared.

Accordingly, the Stroop effect was reflected by large and robust reaction time differences between the incongruent and the congruent condition. The differences were present in the immediate naming (Chapter 5.1, Exp. 1) as well as the delayed naming experiments (Chapter 5.1, Exp. 2 and Table 6.2).

The behavioural findings were interpreted to indicate a strong cognitive conflict in the incongruent condition, which was reflected by increased reaction times.

However, the findings from the reaction time pattern were not reflected by the BOLD signal.

Reverse Stroop effect The neural pattern of the reverse Stroop effect speaks to the notion that the cognitive demand in the congruent condition during the counting phase of the delayed paradigm was actually higher than the demand in the incongruent condition. On the other hand, decreased reaction

time latencies for the response phase suggest that the conflict was apparently solved at the response phase, but the facilitation effect was not reflected by neural substrates.

For the **reverse Stroop effect** (congruent > incongruent) brain activity was increased in the right ventrolateral prefrontal cortex (VLPFC) comprising the inferior frontal gyrus (IFG) and inferior frontal junction (IFJ) (see Table 6.2, Figure 6.5). The percent signal change graph further indicates that the activity in the right IFJ was actually increased during the counting phase of the congruent condition (see Fig. 6.6). Finally, activity on the junction of the right occipital and inferior parietal cortex is observed, the region is also known as temporo-occipito-parietal junction (TPJ).

These regions are well known for their involvement in the resolution of conflict, the detection of salient cues, in switching and dividing attention, particularly when irrelevant objects, either globally or locally, must be put aside and the information must be maintained (Chang et al., 2013; Cieslik et al., 2015; Krall et al., 2014).

The right VLPFC, including the IFG and the IFJ, is typically involved in tasks with an increased demand in cognitive control, namely tasks which involve motor inhibition, response inhibition, reflexive orienting and the processing of salient cues (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010; Swann et al., 2012; Barber, Caffo, Pekar, & Mostofsky, 2013). For instance, according to a meta-analysis by Levy and Wagner (2011), the right VLPFC, including pars opercularis (BA 44) and inferior and middle frontal gyri, is consistently found active in motor inhibition tasks; the same ventrolateral prefrontal region, including the right inferior frontal junction (IFJ), is reported to be involved in the processing of reflexive reorienting.

In tandem with frontal regions, the right TPJ is assumed to be involved in stimulus-driven attentional orienting and the detection of salient events outside the current focus of attention (Corbetta & Shulman, 2002; Chang et al., 2013). It is reported to be co-activated with the inferior frontal junction in an ALE meta-analysis by Krall et al. (2014) for attention shifting and reorienting. Among others, the IFJ and the TPJ showed significant convergence across seven different tasks investigating cognitive control of actions (namely Stroop, Flanker, Simon, SRC[2], antisaccade[3], go/no-go and stop-signal tasks) in a meta-analysis by Cieslik et al. (2015).

In the present study, activity in the right TPJ was not only observed during Numerical Stroop task but also during the Picture-Word Interference task. Consequently the activity of the TPJ will further be discussed in Chapter 6.6, in which the results of the paradigms are compared.

Finally, the right temporo-parietal cluster also incorporates a right inferior parietal region (see Table 6.2 and Figure 6.2). As mentioned previously, initially inferior parietal activity was expected to reflect the conflict due to the numerical incongruence of the target and the distractor. Therefore, enhanced inferior parietal activity was supposed to be observed in the incongruent condition and not in the congruent condition.

However, the results suggest that the processing demand was actually higher in the congruent condition.

Presumably, an additional demand in the congruent condition was driven by the participants' attempt to align the magnitude of the quantity and the number word and to decide whether they were off balance or not, which was presumably more demanding for the close magnitudes and therefore, eventually even more so for the identical magnitudes.

Furthermore, during the retrieval phase of the congruent condition, the participants were eventually struggling to disentangle the magnitude of the quantity and the number provided by the distractor word and to integrate both into one response.

During the response phase the integration process was apparently terminated and the correct response was prepared: Compared to the incongruent and the neutral condition, in which two responses were initialized, reaction times for the congruent condition were decreased. However, the facilitation effect in the response phase of the congruent condition was not depicted by neural correlates.

Conclusion The activation pattern for the **interference effect** resembles the one obtained with the reaction times in the Number Stroop task: Behaviourally, in the immediate naming paradigm, the reaction times for the incongruent and the neutral condition differed significantly (see Chapter 5.1.3, Exp. 1), but they did not differ in the delayed naming paradigm (see Chapter 5.1.3, Exp. 2). The neural activation

[2]Stimulus-Response Compatibility

[3]According to Cieslik et al. (2015) in an antisaccade task, "participants are instructed to fixate a central position and, after the presentation of a lateralized target stimulus, to perform a saccadic eye-movement (antisaccade) to its mirror-symmetrical position. Participants usually show increased reaction times and error rate when instructed to perform an antisaccade compared to a prosaccade (eye-movement to the lateralized target)".

pattern is consistent with the behavioural results: a neural correlate for the interference effect is observed during the retrieval phase, but not during the response phase. Consequently, the findings are interpreted to reflect competition during the early counting phase.

The results from the **reverse Stroop effect** suggest that the counting process is hampered in the congruent condition.

Interestingly, only for the reverse Stroop effect increased activity in the inferior parietal cortex is found. Because the inferior parietal lobe was suggested to reflect an increased demand due to numerical processing, the result suggests that the effort in the incongruent was exceeded by the numerical demand in the congruent condition. However, an alternative interpretation of inferior parietal lobe functions will be discussed in Chapter 7.3.1.

Nevertheless, during the retrieval phase of the congruent condition, activity in a right hemispheric network comprising the inferior frontal gyrus, inferior frontal junction and the temporo-parietal junction supports the assumption of a high processing demand. The network is consistently reported to reflect Stroop conflicts and is therefore interpreted to strongly indicate increased cognitive control (Cieslik et al., 2015).

The right horizontal segment of the intraparietal sulcus (hIPS) constitutes a component of the Numerical Stroop task network, but it is not found susceptible to the specific conflicts as induced by the task. However, activity in the right IPS was observed during the retrieval phase of the reverse Stroop contrast and also interpreted to depict an increased numerical processing demand. Activity of the ACC was not observed.

We may assume cautiously that, first, inhibitory processes in the Numerical Stroop task are present in the incongruent and in the congruent condition and second, that these conflicts originate during the retrieval phase.

However, during the response phase, no neural results were obtained. In particular, it is highly doubtful why the strong inhibitory effect of the incongruent condition during the response phase, which was consistently found to increase reaction times (see Chapter 5.1 and Table 6.2), was not reflected by neural activation. Accordingly, we must still acknowledge the possibility that the temporal succession of the two stages in the trials was too close to be able to conceive a difference in the slow-acting BOLD signal.

6.3 Picture-Word Interference

6.3.1 Methods

Participants

The PWI was conducted with the same sample and in the same session as the Numerical Stroop (see Chapter 6.1).

6.3.2 Material

The set consisted of 33 pictures by Rossion and Pourtois (2004). Stimulus set B from the behavioural experiment (see Chapter 5.3 on p. 55) was used. The stimuli are presented in the Appendix, Table A.2. Due to a low naming agreement in the pilot studies, the picture "eagle" was replaced by "peacock" and the picture "peach" was substituted by "pear". The distractors were redistributed accordingly.

Each picture was presented five times: twice with two different related distractors, twice with two different unrelated distractors and once with the original name, resulting in a total of 165 experimental stimuli.

In the *related* condition, picture and distractor word were semantically related, e.g., "sheep" and GOAT or "sheep" and PONY. In the *unrelated* condition, the distractors were randomly redistributed to obtain picture-distractor word combinations which were semantically unrelated, e.g., "sheep" and COMET or "sheep" and DIPPER. In the related and the unrelated condition, the picture name and the word did not start with the same onset, i.e. they were not phonologically related. In the *same* condition, the distractor designated the picture, e.g., "sheep" and SHEEP.

In addition to the set of 165 experimental items, between 39 and 57 null trials were presented. The number of null trials varied slightly, because number, order and length of the null trials was automatized by Optseq2 (Dale, 1999). In total, in the PWI experiment between 204 and 222 items were presented to each participant.

The experiment was conducted in German, all distractor words were German and written in capitals.

In this MRI experiment, picture and distractor were always presented simultaneously. Usually, the distractor was superimposed on the picture. Because of the dark colour of ten pictures, to increase the visibility of the distractor, the word was presented below the picture.

Thirty-three filler items were randomly chosen from the stimulus set and counterbalanced across participants.

Procedure

The procedure for the PWI was identical to the one used for the NSP (see Chapter 6.1)

6.3.3 Data Acquisition and Analysis

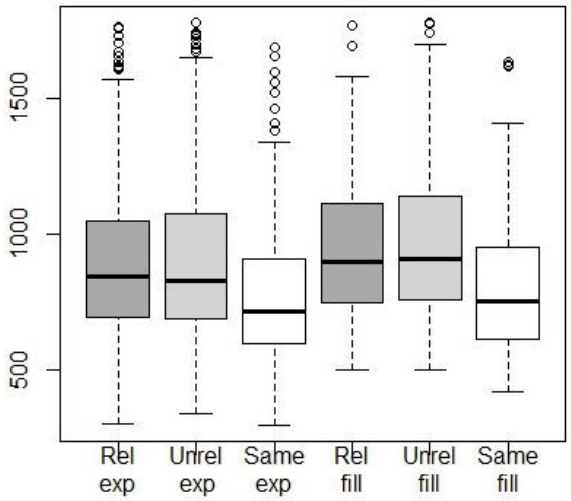
The data acquisition and the analysis of the data was identical for the PWI and the NSP (see Chapter 6.1).

In accordance with the numerical Stroop task, the final model included six experimental task regressors, six filler task regressors, an error term, the null events and six motion parameters.

As described in the previous Chapter 6.1 from the frequency distribution of the Monte-Carlo simulation with 10,000 iterations the cluster size (107 voxel) that occurs $<1\%$ of the time by chance was selected, to give a threshold of $p < .05$ (corrected).

6.3.4 Behavioural Results

Figure 6.7: Picture-Word Interference Task response latencies



condition			
experiment ('picture')			
	mean(ms)	SD	error
related	893	(264)	3.6%
unrelated	899	(285)	4.3%
same	768	(246)	3.0%
	869	(274)	
filler ('distractor')			
related	936	(249)	5.4%
unrelated	970	(284)	2.2%
same	822	(275)	1.1%
	926	(274)	

Mean reaction times (RTs) are given in milliseconds (ms), with the standard deviation (SD) in parentheses. RTs were obtained during functional imaging. The overt responses were processed with a positive low pass filter to reduce scanner noise and onsets were determined with Checkvocal (Protopapas, 2007).

Error

The reaction time data was processed in the same manner as described in Chapter 6.1.

Items were coded as inaccurate and excluded from analysis for the following reasons: missing or delayed response (later than 2 seconds after cue presentation), self-corrections, naming the distractor in the experimental condition or the picture in the filler condition, wrong picture name, noisy recording. Mean reaction times and error rates are presented in 6.7. 6.4% of the answers were erroneous.

Pearson's χ^2 tests using the software *R* (Version 3.0.2) (R Core Team, 2014) showed that the error rates did not differ significantly across conditions, neither over the entire experiment ($\chi^2(5) = 10.033, p = .07$), nor exclusively for picture naming ($\chi^2(2) = 1.923, p = .38$).

Analysis

The behavioural analysis of the data was identical for the PWI and the NSP (see Chapter 6.1).

Results

During the retrieval phase of the Picture-Word Interference task, the target picture was presented simultaneously with a related, unrelated or identical ('same') distractor word. The participant's response was postponed until the cue was shown. In the experimental condition a blue cue indicated to name the picture. In the filler condition ('read'), a red cue indicated to utter the distractor word. The mean reaction times which were obtained during the fMRI scanning procedure are presented in Figure and Table 6.7.

Overall, reaction times are influenced by the relatedness of target and distractor ($\chi^2(2) = 52.63$, $p < .0001$). Compared to the experimental condition, naming latencies are longer in the filler condition ($\chi^2(3) = 31.87, p < .0001$). But the combined impact of condition and cue does not influence the naming latencies ($\chi^2(4) = 0.58, p = 0.74$).

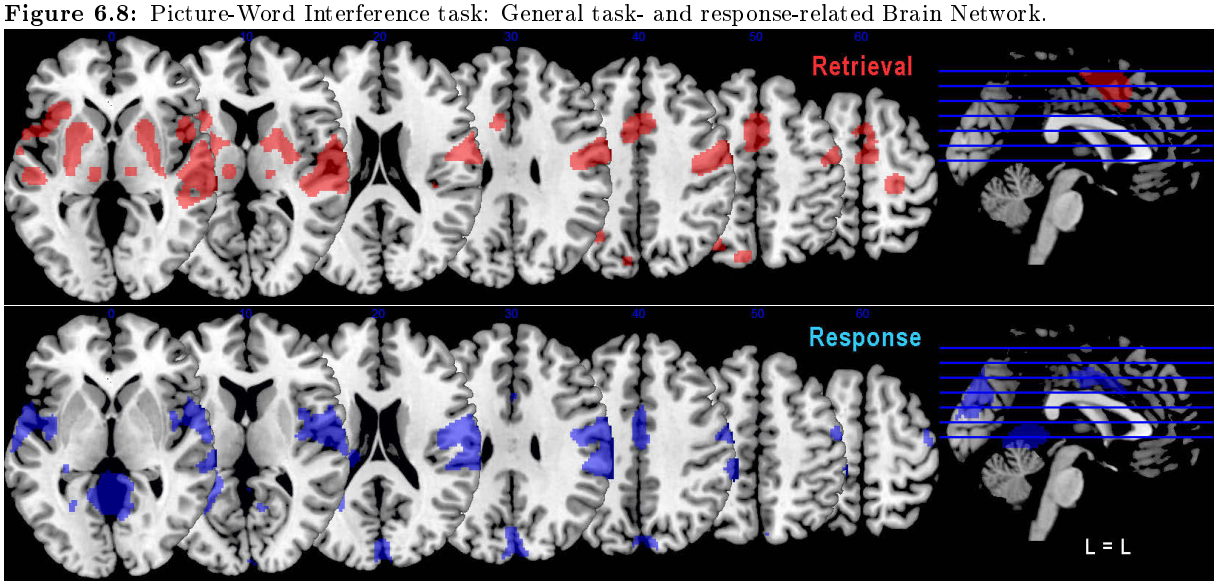
Post hoc test revealed that reaction times were increased in the *related* condition compared to the *same* condition, for picture naming ($b = 0.1664, t(26) = 9.874, p < .0001$) as well as for distractor reading ($b = 0.142, t(26) = 4.772, p < .001$). Reaction times were also increased in the *unrelated* condition compared to the *same* condition, for picture naming ($b = 0.1740, t(26) = 10.316, p < .0001$) as well as for distractor reading ($b = 0.1618, t(26) = 5.433, p < .0001$). Reaction times did not differ for the *related* condition and the *unrelated* condition, neither for picture naming ($b = -0.008, t(26) = -0.510, p = .99$) nor for reading the distractor ($b = -0.0194, t(26) = -0.765, p = .97$).

6.3.5 Functional Imaging Results

We aimed to identify the brain network, in which activation is modulated by the lexical retrieval process (*task*) and the naming procedure (*response*).

General Task- and Response-related Brain Network While the participants retrieved the picture name (task> implicit baseline), enhanced activity in bilateral postcentral und superior temporal gyri was observed (see Table 6.3 and Figure 6.8). In addition, activity of the left ventrolateral prefrontal cortex (VLPFC), left inferior parietal cortex and thalamic activity is found. Also during the response phase of the task, bilateral superior temporal activity is observed, which is supplemented by activation in the cerebellum, cuneus and middle cingulate cortex. During the task *and* the response phase, a large region centred at the rolandic opercula (BA 43) is active in both hemispheres (see Appendix, Table A.5), embracing the bilateral primary auditory cortex.

Figure 6.8: Picture-Word Interference task: General task- and response-related Brain Network.



Whole-brain results were obtained post stimulus onset ('retrieval phase' = red) and post cue onset ('response phase' = blue). MNI coordinates derived from T-maps with T > 3.17, at a cluster-corrected significance threshold of p < .05, with a minimum cluster extend of k > 100 derived with p <.001 and displayed with neurological orientation (left = left). The figure was created with Mricron (Rorden & Brett, 2000). For the corresponding coordinates, see Table 6.3

Interference The *interference effect* (retrieving picture name in the context of a related compared to an unrelated distractor word) was positively correlated with the BOLD response in the left middle temporal gyrus (see Figure 6.9 and Table 6.4, top), extending to the left Angular Gyrus. A negative correlation (i.e. reverse interference effect) was not observed.

Stroop For the *Stroop effect* (related > same), during the *retrieval phase* (see Figure 6.10, red areas, and Table 6.4), the BOLD signal was mainly associated with a huge neural network in the left hemisphere, in particular, with the inferior frontal gyrus, including the pars triangularis and opercularis (Broca's area), which is associated with phonological and syntactic processing and speech-related working memory tasks (Binder et al., 2009), in particular for word retrieval during speech production (Price, 2012). Also the left superior and inferior parietal lobe, including the left Angular Gyrus (PGa), is considered to play a crucial role in semantic processing (Binder et al., 2009). Additional activity in the left SMA, right insula and bilateral precentral gyri was observed.

Activity of the same area in the right inferior frontal area, with the right insula, was also observed during the *response phase* of the Stroop contrast (see Table 6.5 and blue areas in Figure 6.10). This phase was also associated with activity in the right inferior parietal and Angular Gyrus. In addition, the left lentiform nucleus in the basal ganglia was found active.

For the *reverse Stroop effect* (same > related), a BOLD response was detected only for the *retrieval phase*, but not for the response phase (see Table 6.4 and Figure 6.11). It was significant in a right parietal, more particular, in the supra-marginal lobe and in the left superior temporal and Angular Gyrus.

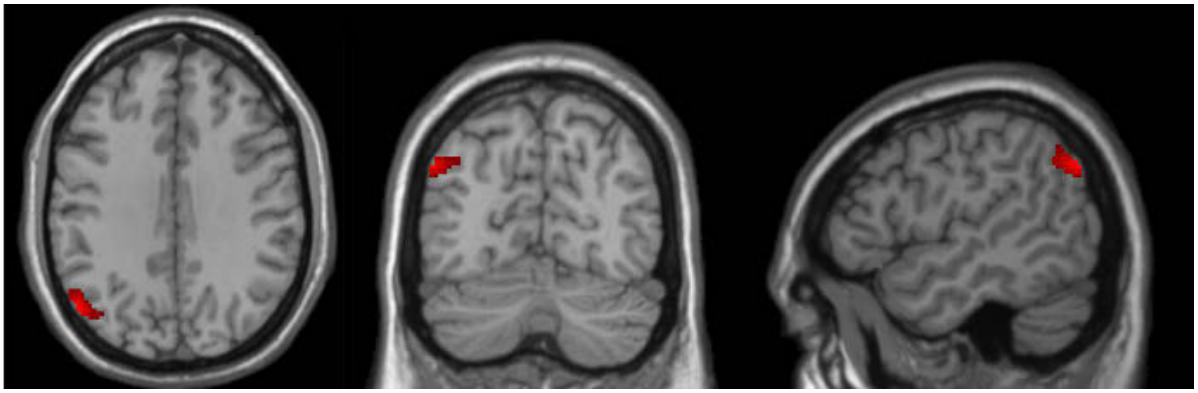
A conjunction of the reverse Stroop with the same > unrelated contrast ($same > rel \wedge same > unr$) revealed (see Table 6.6, 'same > conflict') that the activity in the right parietal and left temporal areas for both contrasts was nearly concordant. A similar result was retrieved for the conjunction of the Stroop contrast with the unrelated > same contrast. The results are displayed in Table 6.6 under the term 'conflict > same'. For the related, as well as the unrelated condition, left inferior parietal and middle and inferior frontal activity was observed. Finally, activity in the left Angular Gyrus was observed for the conjunction of the related and the same condition with the unrelated condition. Because in both, the related as well as the same condition, the distractor was semantically close to the picture name, the conjunction was termed 'semantic proximity' (Table 6.6).

Table 6.3: Neural network for task and response in the Picture-Word Interference task.

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Task > null					
Left postcentral and	-48	-12	34	12.04	5515
superior and inferior temporal gyrus (6/22)	-58	-6	28	11.71	
	-52	-20	4	6.58	
Right postcentral and	62	-2	22	11.58	4830
superior and inferior temporal gyrus (6/22)	52	-8	34	10.58	
	50	-22	8	7.00	
VLPFC and	-2	0	58	8.72	1326
middle and anterior cingulate cortex (6/24)	-6	6	40	6.65	
	2	14	48	6.04	
Right postcentral gyrus (Area 6)	22	-26	60	7.29	124
Left inferior parietal lobe (hIP1) (7/40)	-38	-50	48	6.20	1348
	-34	-58	46	6.18	
	-8	-76	48	4.82	
Left thalamus	-12	-20	4	5.97	187
Cue > null					
Left superior temporal and	-62	0	2	10.82	3976
postcentral gyrus (22/ 42)	-66	-22	14	10.38	
	-64	-4	18	7.62	
Right superior temporal and	64	0	4	9.72	4318
supra-marginal gyrus (6/40)	66	-8	6	9.45	
	66	-22	18	8.91	
cerebellar vermis	2	-50	2	6.94	2575
	-22	-44	12	5.77	
	-14	-60	-18	5.48	
cuneus (19)	6	-84	40	6.59	637
	4	-90	28	5.64	
occipital gyrus (calcarine gyrus)	4	-96	12	4.61	
middle and anterior cingulate cortex (24)	0	-10	40	5.42	330
	0	4	38	4.56	

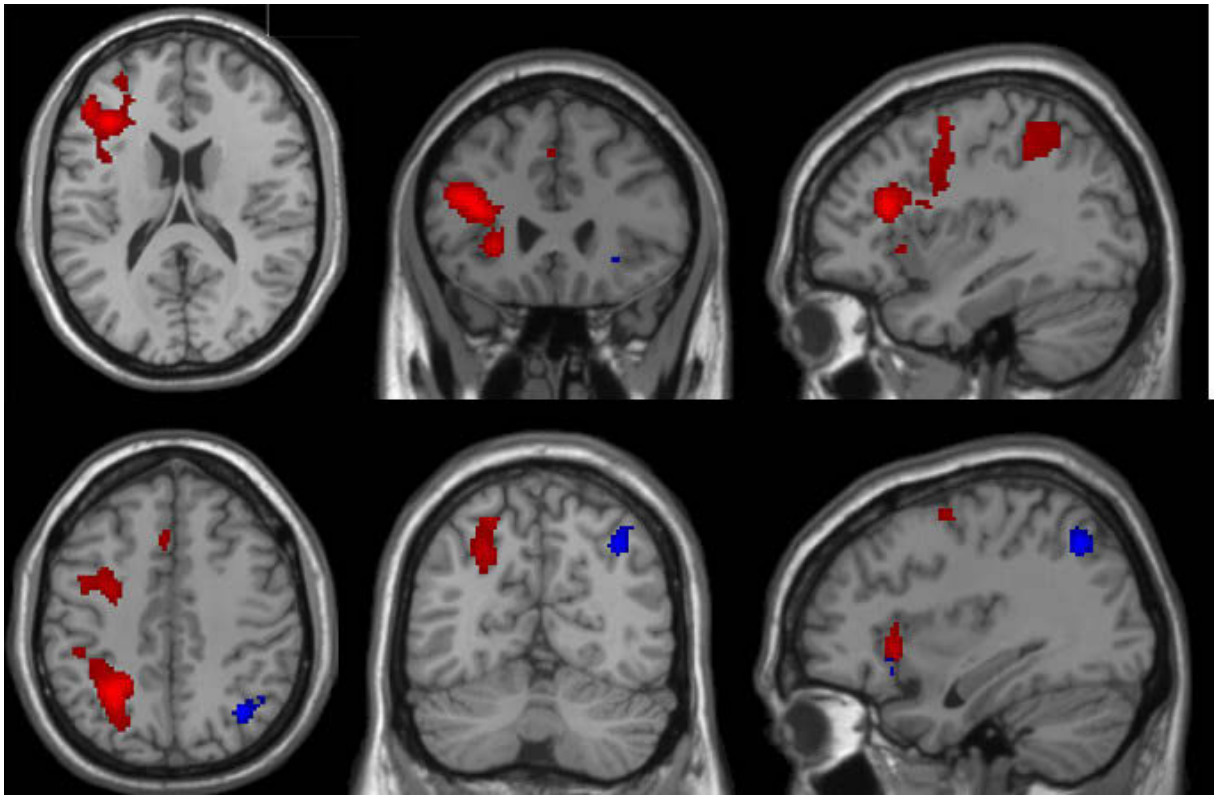
Results were obtained post stimulus onset ('task') and post cue onset ('response'). MNI coordinates derived from T-maps with T > 3.17, at a cluster-corrected significance threshold of $p < .05$, with a minimum cluster extend of $k > 100$ derived with $p < .001$. Labelling was provided by the Anatomy toolbox (Eickhoff et al., 2005), Brodmann areas in parentheses. For the corresponding images, see Fig. 6.8.

Figure 6.9: Interference effect in the Picture-Word Interference task



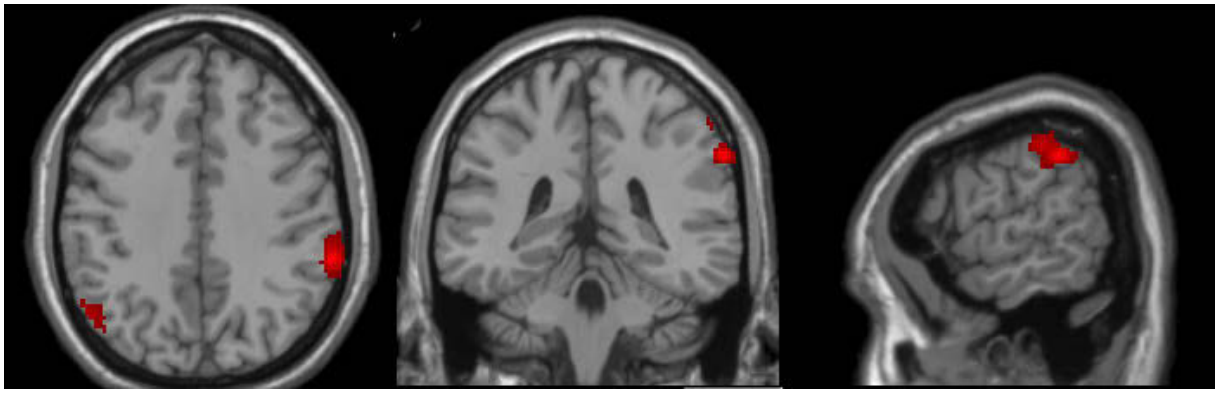
Whole-brain results were obtained post stimulus onset ('retrieval phase'). Displayed with neurological orientation (left = left). MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < 0.05$, with a minimum cluster extend of $k > 107$ derived with $p < .001$. Figure created with FIVE (Schultz & McLaren, 2014). For the corresponding coordinates, see Table 6.4, first paragraph.

Figure 6.10: Neural network for the Stroop effect in the Picture-Word Interference task



Whole-brain results were obtained post stimulus onset ('retrieval phase' = red) and post cue onset ('response phase' = blue). Displayed with neurological orientation (left = left). MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < 0.05$, with a minimum cluster extend of $k > 107$ derived with $p < .001$. Figure created with FIVE (Schultz & McLaren, 2014). For the corresponding coordinates, see Table 6.4 and 6.5, third row.

Figure 6.11: Neural network for the reverse Stroop effect in the Picture-Word Interference task



Whole-brain results were obtained post stimulus onset ('retrieval phase'). Displayed with neurological orientation (left = left). MNI coordinates derived from T-maps with T > 3.17, at a cluster-corrected significance threshold of p < 0.05, with a minimum cluster extend of k > 107 derived with p <.001. Figure created with FIVE (Schultz & McLaren, 2014). For the corresponding coordinates, see Table 6.4, 4th row.

Table 6.4: Retrieval phase in the Picture-Word Interference task.

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Interference effect (related > unrelated)					
Left posterior middle temporal gyrus (37) and	-52	-70	34	4.90	214
Angular Gyrus (39)	-48	-62	46	4.10	
	-40	-76	40	3.87	
Reverse Interference effect (unrelated > related)					
	n.s.				
Stroop effect (related > same)					
Left inferior frontal (p. triang. and opercul.) (44,45)	-38	26	18	6.74	2096
and precentral gyrus (6)	-48	28	22	6.21	
with inferior frontal junction	-44	4	34	5.84	
Left inferior and superior parietal lobe (hIP3, PGa, 7a)	-30	-52	42	6.70	1207
and middle occipital gyrus (19)	-30	-72	32	5.03	
	-24	-64	56	4.64	
Left dorsomedial prefrontal cortex (6)	-6	16	52	5.57	295
and SMA	-4	8	58	4.50	
	-4	22	44	3.86	
Right insula	34	22	-2	4.80	124
Right superior frontal gyrus (6)	26	-4	56	4.53	126
Reverse Stroop effect (same > related)					
Right supra-marginal gyrus (IPC/PF) (40)	62	-38	38	5.27	281
	58	-34	50	4.38	
	60	-28	44	4.27	
Left Angular and	-54	-66	36	4.21	130
superior temporal gyrus (39)	-54	-60	42	3.89	
	-60	-60	26	3.28	

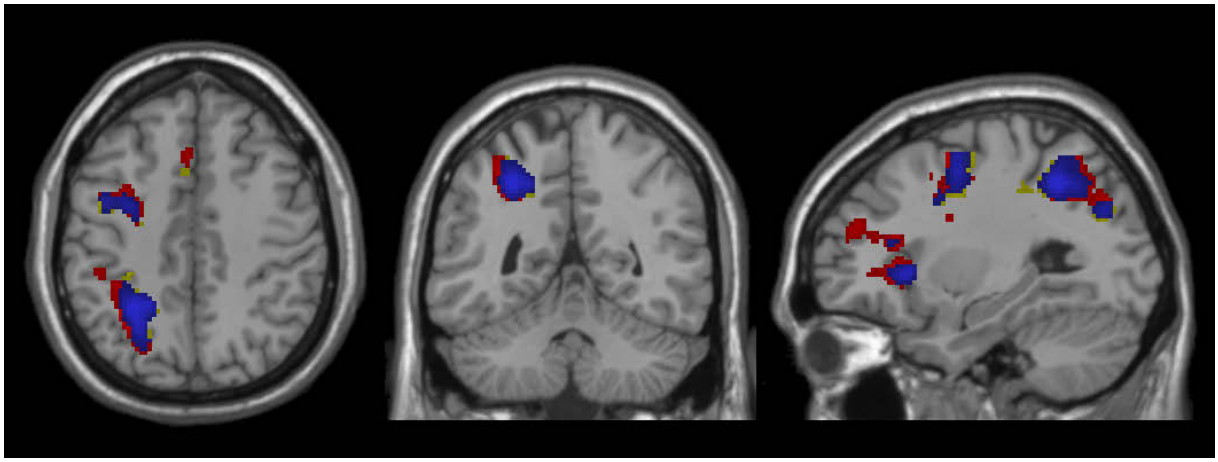
Whole-brain analysis results of the *retrieval phase* for the Picture-Word Interference task. Results were obtained by post stimulus onset. MNI coordinates derived from T-maps with T > 3.17, at a cluster-corrected significance threshold of p < 0.05, with a minimum cluster extend of k > 107 derived with p <.001. Labelling was provided by Talairach Daemon (Lancaster et al., 2000) and the Anatomy toolbox (Eickhoff et al., 2005). SMA = supplementary motor area

Table 6.5: Response phase in the Picture-Word Interference task.

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Interference effect (related>unrelated)					
	n.s.				
Reverse Interference effect (unrelated > related)					
	n.s.				
Stroop effect (related > same)					
Right Angular Gyrus and	34	-64	44	4.54	149
inferior parietal lobe (7,40)	44	-54	40	3.72	
Right insula and	38	18	-2	4.40	107
inferior frontal gyrus (pars orbit.) (47)	30	22	-10	4.17	
	36	22	-16	4.01	
Left Lentiform Nucleus (Pallidus and Putamen)	-24	-14	2	4.39	120
	-28	0	2	4.00	
	-26	-14	-6	3.33	
Reverse Stroop effect (same > related)					
	n.s.				

Whole-brain analysis results in the *response phase* of the Picture-Word Interference task. Results were obtained by post cue onset. MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < 0.05$, with a minimum cluster extend of $k > 107$ derived with $p < .001$. Labelling according to the Anatomy toolbox (Eickhoff et al., 2005), Brodmann areas provided by the Talairach Daemon (Lancaster et al., 2000).

Figure 6.12: PWI fMRI results: Mutual activity for Conflict (rel + unr) > same



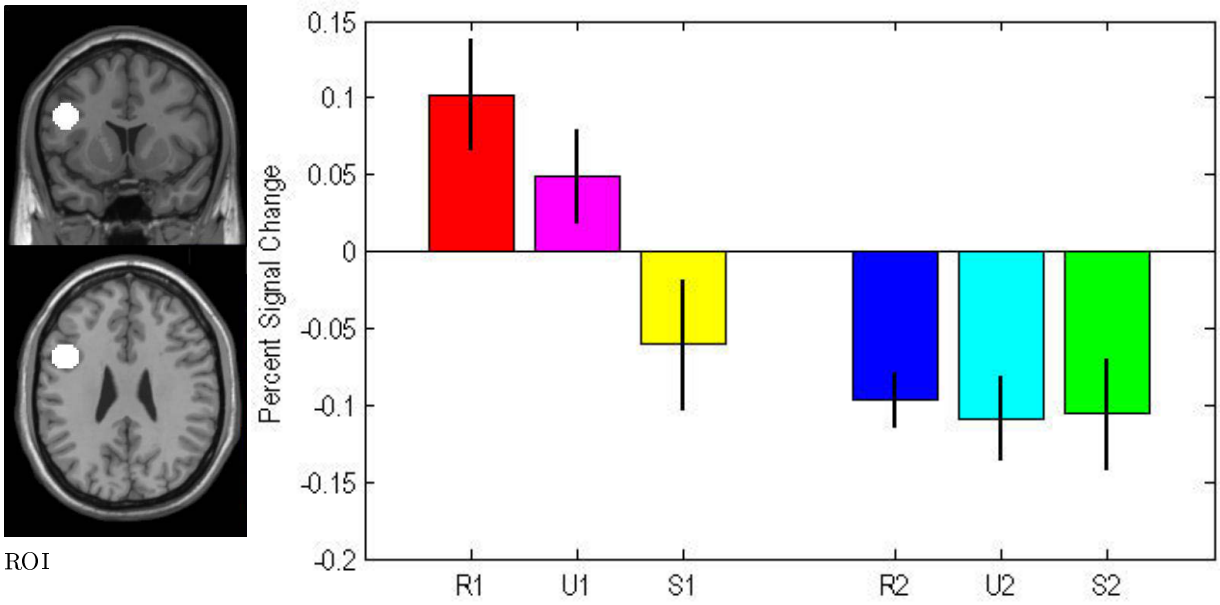
Results for rel>same in red, for unr>same in yellow. Results of the conjunction $rel > same \wedge unrel > same$ for the Picture-Word Interference task in blue. Whole-brain analysis results were obtained post stimulus onset ('retrieval phase'). Displayed with neurological orientation (left = left). Figure created with FIVE (Schultz & McLaren, 2014). For the corresponding coordinates, see Table 6.6.

Table 6.6: PWI retrieval phase: (1) Conflict > base, (2) Base > conflict and (3) Semantic > unrelated

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Conflict > Baseline (rel + unr > same)					
Left inferior parietal [hip3] (7)	-30	-50	44	5.69	720
and middle occipital lobe	-22	-48	44	5.19	
	-28	-74	32	4.57	
Left precentral (6)	-44	0	50	5.39	548
and middle frontal gyrus	-32	-2	50	5.13	
	-26	-4	58	4.98	
Left dorsomedial prefrontal cortex (6)	-6	16	50	5.37	203
and SMA	-2	10	56	4.43	
	8	10	54	3.77	
Left insula	-30	22	0	5.12	129
Left inferior frontal gyrus (pars triang.) (45/46)	-46	26	22	4.52	199
	-34	28	16	3.82	
Same > Conflict (same > rel + unr)					
Right inferior parietal lobe (40)	62	-38	38	5.27	253
and supra-marginal gyrus	58	-34	50	4.38	
	62	-30	42	4.19	
Left Angular Gyrus (39)	-54	-66	36	4.21	130
and superior temporal gyrus	-54	-60	42	3.89	
	-60	-60	26	3.28	
Semantic Proximity > Unrelated (rel + same > unrel)					
Left posterior temporal and	-52	-70	34	4.90	202
Angular Gyrus [PGp] (39)	-48	-62	46	4.10	
	-40	-76	40	3.87	

Picture-Word Interference conjunctions: (1) Conflict > Same ($rel > same \wedge unrel > same$) (top), (2) Same > conflict ($same > rel \wedge same > unrel$) (3) Semantic proximity > unrelated ($rel > unr \wedge same > unr$) (bottom). Results were obtained post stimulus onset. The *MS/CN* conjunction as defined by Nichols et al. (2005) and as implemented in SPM8 (*Statistical Parametric Mapping*, 2009) was performed. Brodmann areas provided by Talairach Daemon (Lancaster et al., 2000) and Anatomy toolbox (Eickhoff et al., 2005) [in square brackets].

Figure 6.13: Picture-Word Interference task: Percent Signal change of beta weights within left IFJ



ROI

Inferior frontal junction ROI defined with rfxplot, as an 8 mm sphere at MNI coordinates [-46, +6, +36] (Brass et al., 2005), resulting in 513 voxel, which were included in the analysis. Significant differences: R1>S1 and U1>S1. R=related, U=unrelated, S=same / 1=retrieval, 2=response.

6.4 Discussion

The present study aimed to investigate the neural representations of the conflicts in the Picture-Word Interference task during the lexical retrieval and the response phase.

During the retrieval and the response phase of the Picture-Word Interference task, the bilateral postcentral gyri are found active (see Appendix, Table A.5). The gyri also include Heschl's gyrus, which is considered to play a key role in language processing in particular in the processing of entire word forms (cf. Chapter 3 *Word Production*).

During the retrieval phase (see Table 6.3 and Figure 6.8), the ventrolateral prefrontal cortex (VLPFC) and inferior temporal cortex are found active. The inferior temporal lobe is considered a key region for object recognition (DiCarlo et al., 2012, cf. Figure 2.1). In particular in tasks which require the categorization and identification of objects and the preparation of motor responses, the VLPFC seems to be involved (Riesenhuber & Poggio, 2000). In addition, the VLPFC is considered to facilitate the recognition of familiar objects by providing long-term memory functions which may also guide the selection of target items among competitors (Akirav & Maroun, 2006; Badre et al., 2005). Finally, the top-down semantic information from the VLPFC is considered to facilitate object recognition in the bilateral inferior temporal cortex (Bar et al., 2006).

During the retrieval and the response phase of the task (see Table 6.3 and Figure 6.8), activity in the anterior cingulate cortex (ACC) is observed. As mentioned earlier (cf. Chapter 3 *Word production*), the ACC is associated with response conflicts (Gasquoine, 2013; Shenhav et al., 2014) and more particular with response suppression in speech production (Price, 2012).

6.4.1 Semantic Interference

During the encoding phase, a left hemispheric portion of the middle temporal gyrus (MTG) – extending to the Angular Gyrus – is found active (Table 6.4 and Figure 6.9). During the response phase, however, no brain activity changes are detected. As stated before (see Chapter 3 *Word production*), the left MTG is considered as one of the core systems in word production (Indefrey, 2011) and particularly involved in lexical retrieval (Friederici, 2012; Indefrey & Levelt, 2004; Indefrey, 2011). Therefore, the left MTG was expected to be responsive to semantic interference.

Numerous PWI studies observed activity in the left middle temporal gyrus (see Chapter 4.1.2 *Object Stroop*). It was, for example, detected for semantically related compared to neutral distractors (a row of 'XXX') (De Zubicaray et al., 2001), it was active, along with the left cuneus and postcentral parietal

lobe, for associative versus unrelated distractors (Abel et al., 2009) and for categorically related and part-whole related distractors compared to unrelated ones (Diaz et al., 2014).

In particular, posterior temporal activity was observed for related compared to unrelated distractors (Kotz et al., 2002) and for categorically homogeneous compared to heterogeneous blocked cycles (De Zubicaray et al., 2014).

I conclude that increased activity in the left MTG may indeed reflect semantic interference during lexical retrieval.

That said, a portion of the left MTG – centred at the MNI coordinates [-52, -70, 34] in the posterior part of the temporal lobe extending to the Angular Gyrus –, which was found active for the interference contrast, was also observed for the *same > related* and *same > unrelated* conjunction (see *reverse Stroop contrast* Table 6.4 and Fig. 6.11 and *same>conflict* conjunction in Table 6.6 and Fig. 6.12.).

This is surprising at first sight, because behaviourally, the *same* condition was responded to faster relative to the *related* and *unrelated* condition. Hence, the left MTG was expected to reflect semantic interference -, but not semantic facilitation effects. However, the brain activation in same and related trials shows a significant overlap in the left temporal gyrus, suggesting a similarity in the neural basis underlying these trials. As previously discussed in the Chapter 4.1.2 *Object Stroop*, activity of the left temporal gyrus has not only been observed in the context of categorical distractors (De Zubicaray et al., 2001; Schnur et al., 2009), but also for associative (Abel et al., 2012), functional (Muehlhaus et al., 2014) and part-whole related distractors (Diaz et al., 2014; Muehlhaus et al., 2014). Also posterior temporal activity was not only observed for semantic-categorical distractors (Kotz et al., 2002; De Zubicaray et al., 2014), but also for phonological and part-whole related distractors (Diaz et al., 2014).

Functional, associative and part-whole related distractors were also reported to facilitate picture naming (Abel et al., 2012; Diaz et al., 2014; Muehlhaus et al., 2014).

The present results thus imply that the left temporal gyrus is not solely responsive to semantic interference, i.e. to the competition of lexical items, but it may rather be involved in the resolution of close semantic proximity between target and distractor in general.

The similarity of the neural response for the related and the identical condition may eventually provide a basis for common, underlying priming effects, namely due to conceptual facilitation (Abdel Rahman & Melinger, 2009) or semantic facilitation (Finkbeiner & Caramazza, 2006; Mahon et al., 2007). This will be discussed further in Chapter 7.

6.4.2 Stroop Effect

Retrieval During retrieval, the Stroop conflict activates a wide left hemispheric network, including inferior frontal (pars triangularis, BA 45) and precentral gyrus. Also the left superior and inferior parietal lobe and the left SMA are involved. In addition, right hemispheric activity in the anterior insula and the superior frontal gyrus is observed (Table 6.4 and Figure 6.10).

As expected, the left inferior frontal gyrus seems to be involved in semantic processing, hence, in the production of words and, more particular, in picture naming. In language related research, the left pars triangularis (with pars opercularis, BA 44) in the inferior frontal gyrus (IFG) is also referred to as Broca's area.

For instance, according to Indefrey and Levelt (2004), the left IFG is found active when picture naming is compared to word generation, but not for overt responses in general. The involvement of the IFG in semantic processing is also stressed in the meta-analysis by Binder et al. (2009). More particular, it may be responsive to increased task difficulty, which is attributed to working memory and phonological processing demands.

As we can see from the conjunction $related > same \wedge unrelated > same$ (see Table 6.6, top row), the pars triangularis is not only active for the related, but also for the unrelated condition. It therefore seems to reflect the higher cognitive demand elicited by the processing of two lexical items versus one item (same condition). This finding is in line with the assumption "that it is not retrieval of semantic knowledge *per se* that is associated with left IFG activity but rather selection of information among competing alternatives from semantic memory" (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997, p. 14792, original emphasis)

The left IFG is also assumed to play a dominant role in language related working memory tasks. In a study by Makuuchi et al. (2009), the non-syntactic working memory (WM) was neurally dissected from the syntactic WM. Whereas the left pars opercularis was reported to be responsive to WM load elicited by syntactically hierarchic structures, two clusters in the LIFS (left inferior frontal sulcus) responded to increased demand in the non-syntactic verbal working memory condition. The clusters peaked in (a)

[-45 27 27] and (b) [-45 9 36]. Interestingly, both clusters in the LIFS are found active in the related compared to the same condition (Stroop contrast). The more anterior cluster (a) was also found active for the *unrelated* > *same* contrast and for the corresponding conjunction (*related* > *same*) ∧ (*unrelated* > *same*). The LIFS is also reported to be correlated with increased naming latencies in the Picture-Word Interference task by Diaz et al. (2014). These findings support the notion that the LIFG indeed reflects an increased WM load, which is evoked by the effort to memorize the two items.

Furthermore, also activation of the left inferior parietal cortex and the left dorsomedial prefrontal cortex (DMPFC) is not restricted to the Stroop effect, i.e. related > same contrast, but also observed in the unrelated>same contrast (conjunction *related* ∧ *unrelated* > *same*, Table 6.6). Both regions are considered to play key functions in language processing and, more particular, in word production (see Chapter 3 *Word production*). The intraparietal sulcus (IPS) seems to support verbal working memory functions, for instance, when holding a word (e.g. Makuuchi & Friederici, 2013). Both, the left IPS and the left DMPFC are considered as being part of the large left-hemispheric network which is involved in the conceptual preparation of picture naming (Binder et al., 2009). Arguably, the SMA is involved in articulatory processes (Indefrey, 2011).

Hence, the large left hemispheric fronto-parietal network which is found active during the retrieval phase of the Stroop contrast is mostly congruent with the network from the *related* ∧ *unrelated* > *same* contrast (Table 6.6). The network seems to provide key nodes for language processing and production and is therefore interpreted to reflect the retrieval and integration of two items (related and unrelated condition) as opposed to one item (same condition).

Interestingly, apart from language-specific research, there is some convergence of the brain regions which are found active for the Stroop effect with findings from a meta-analysis on Stroop tasks (Cieslik et al., 2015). The authors report a bilateral network consisting of anterior insula, inferior frontal gyrus - including pars orbitalis and pars triangularis -, precentral gyrus (inferior frontal junction) and a left-hemispheric extension to the superior parietal and inferior parietal lobe and pre-SMA. Albeit, in the present study, these areas are predominant in the left hemisphere.

The inferior frontal junction (IFJ), the pre-supplementary motor area (pre-SMA), the anterior insula cortex, the dorsal pre-motor cortex and the posterior parietal cortex (PPC) are also part of the cognitive control network as proposed by Sundermann and Pfleiderer (2012). Posterior parietal cortex (PPC) activation is consistently reported in cognitive control tasks (Cieslik et al., 2015, 2012; Kim et al., 2012; Kim, Johnson, Cilles, & Gold, 2011; Sundermann & Pfleiderer, 2012).

In accordance with the behavioural reaction time results, the neural activation patterns lead to the conclusion that the related condition was indeed provoking strong conflicts during the retrieval phase of the Picture-Word Interference task. They are reflected by activity in a widely distributed frontal and parietal network. Initially, in particular the inferior frontal junction was expected to be active exclusively during the response phase. The left hemispheric dominance of the network during the retrieval phase most likely reflects the language specificity of the conflict.

Response At the response stage, inferior parietal and inferior frontal (pars orbitalis) activity is found, but the left hemispheric dominance of the network during the retrieval stage is inverted to a right hemispheric dominance at the response stage (Table 6.5 and Figure 6.10). Activity of the inferior frontal gyrus is extended to the anterior insula.

Accordingly, at the response stage convergent activation with networks known to be involved in cognitive and attentional control is found. The findings are also in line with the results from meta-analyses of Stroop tasks, for instance with findings regarding the inferior frontal lobe (Attout et al., 2014; Derrfuss et al., 2005; Kim et al., 2011, 2012; Levy & Wagner, 2011; Sundermann & Pfleiderer, 2012).

Also the right insula, which is found active during the retrieval and the response phase of the Stroop conflict, is assumed to play an important role in cognitive control (Bressler & Menon, 2010; Cieslik et al., 2015; Menon & Uddin, 2010; Sundermann & Pfleiderer, 2012; Uddin, Supekar, Ryali, & Menon, 2011).

Evident from the neural task and response networks (see Table 6.4), the middle cingulate gyrus was actually active during the retrieval and the response phase of the PWI, which may indeed reflect its involvement in response suppression in overt speech (Price, 2012). Contrary to expectation, the cingulate gyrus was not responsive to the Stroop conflict.

Activation in the left basal ganglia, more precisely in the left lentiform nucleus (globus pallidus) was only detected during the response phase, but not during the retrieval phase. The lentiform nucleus is part of a group of subcortical nuclei which form the basal ganglia (BG). The BG are supposed to play a prominent role in motor behaviour, especially in the production of words, as opposed to the generation of nonsense syllables (Crosson et al., 2003). According to Aron et al. (2007) the BG interact

with the inferior frontal cortex, forming a fronto-basal-ganglia network for inhibitory control of action and cognition. Activity of the BG may therefore reflect the suppression of the prepared distractor word during the response phase.

Conclusion The mechanisms of the interference effect and the Stroop effect in the Picture-Word Interference paradigm were examined. Two cognitive stages of the paradigm were differentiated, namely the retrieval and the response phase. Left hemispheric activity in the middle temporal gyrus during the retrieval phase of the interference contrast was interpreted to reflect an increased demand in lexical retrieval which is unlikely to mirror lexical competition but rather the resolution of close semantic proximity. For the Stroop effect, early left hemispheric brain activity in the inferior frontal and inferior and superior parietal lobe is interpreted to indicate an increased cognitive and working memory demand elicited by the retrieval of two lexical items (Indefrey & Levelt, 2004; Binder et al., 2009) as compared to one item, whereas right hemispheric frontal and parietal brain activity is assumed to reflect a response conflict (Cieslik et al., 2015).

6.5 Comparison

The present study aimed to investigate the neural representations of the interference effect and the Stroop effect in two different paradigms, which are based in separate core systems, namely the object and the numerical core system.

The **interference effect** in the Numerical Stroop was associated with right hemispheric activity in the inferior temporal gyrus (Table 6.2), for the corresponding conflict in the Picture-Word Interference task, on the other hand, left hemispheric activity in the middle temporal gyrus was observed (Table 6.4). The results are illustrated jointly in Figure 6.14.

The **Stroop effect** in the Numerical Stroop task was captured with the incongruent>congruent contrast, it did not yield significant results. The Stroop effect in the Picture-Word Interference task elicited activity in a fronto-parietal network which was dominant in the left hemisphere during the retrieval phase and in the right hemisphere during the response phase (Table 6.4 and 6.5).

In both paradigms, **reverse Stroop effects** were obtained. In the Picture-Word Interference task, reverse Stroop effects were captured by the same>related contrast. As previously mentioned, also the same>unrelated contrast and the same>conflict conjunction (i.e. $same > related \wedge unrelated$) yielded significant results (see Table 6.4 and 6.6). Enhanced activity for the reverse Stroop effect was found in bilateral inferior parietal and left posterior temporal brain regions. For the reverse Stroop effect in the Numerical Stroop task, which was captured with the congruent>incongruent contrast (see Table 6.2), enhanced activity in the right inferior frontal and parietal cortex was detected. Frontal-parietal activity was also observed for the congruent>neutral contrast (see Table 6.7). In addition, for the latter contrast enhanced activity in the bilateral fusiform gyrus was detected.

In the present chapter, it was examined, whether there are common neural substrates underlying the paradigms. Joint activity for corresponding contrasts was expected to reveal processes which are convergent across task. Hence, it was investigated whether there are common neural substrates associated with attentional control or regulatory and monitoring processes underlying both core systems.

For instance, in a study by Piai, Roelofs, Acheson, and Takashima (2013), common neural substrates for the conflicts in a Picture-Word Interference task, a Colour-Stroop task and a Simon task were examined with conjunction analyses. Reportedly, for all three tasks the dorsal anterior cingulate cortex (ACC) and left superior temporal gyrus (STG) was active in incongruent trials and suggested to host a 'domain-general attentional control function'. The Colour-Stroop task as well as the Picture-Word Interference task involved overt naming. For both tasks the incongruent condition elicited enhanced activity in the ventral STG, which was therefore interpreted to reflect a language-related control function.

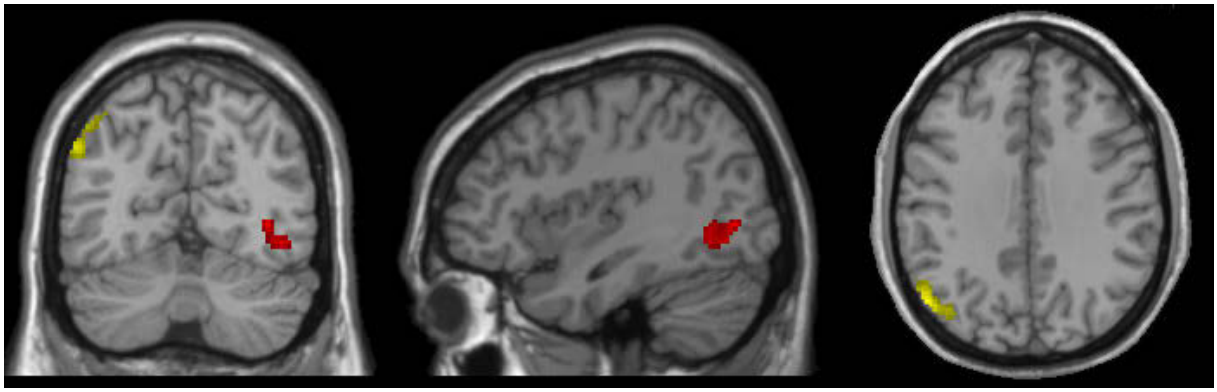
As previously mentioned, also in the present study the ACC and inferior frontal junction were expected to reflect response conflicts across tasks. But contrary to expectations, during the response phase of the Numerical Stroop paradigm (NSP), no neural substrates were detected neither for the interference effect nor for the Stroop effect. Also with conjunction analyses for the response phase across tasks, common neural correlates for the related or incongruent, i.e. conflicting trials, were not observed.

During the retrieval phase of the PWI and the NSP, on the other hand, the interference effect and the Stroop effect were expected to rely on different brain regions (cf. Paragraph 6.0.1 and 6.0.2). Accordingly, common neural substrates were not detected with conjunction analyses.

Also for the conjunction analysis of the reverse Stroop contrast across paradigms, results were not significant.

Finally, only the above-mentioned congruent>neutral and same>unrelated contrasts seem to rely on a common neural substrate, which is located on the junction between the temporal and the parietal lobe (see Table 6.7.)

Figure 6.14: Interference effect in the Numerical Stroop (red) and the Picture-Word Interference task (orange).



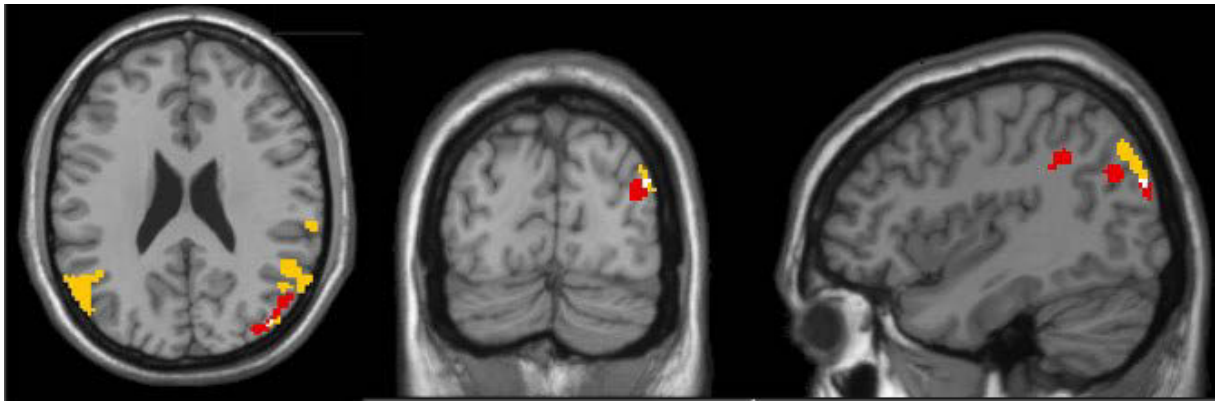
Neurological orientation (left = left). For the corresponding MNI coordinates see Table 6.2 (NSP) and Table 6.4 (PWI).

Table 6.7: NSP & PWI conjunction: NSP ($congruent > neutral$) $\wedge$ PWI ($same > unrelated$)

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
Numerical Stroop task: congruent>neutral					
Left lingual and fusiform gyrus (36)	-20	-40	-9	5.15	241
	-27	-35	-16	3.32	
Right fusiform gyrus (19)	29	-55	-11	5.11	154
	32	-58	-1	4.18	
Right middle occipital gyrus (19)	32	-84	18	5.00	154
and inferior parietal cortex	37	-68	26	4.38	
and middle temporal gyrus (39)	45	-67	20	3.75	
Right inferior parietal (40) and	39	-44	33	4.73	180
and supramarginal gyrus (40)	48	-53	43	3.75	
	50	-50	36	3.38	
Right inferior frontal gyrus (44)	54	10	21	4.44	123
and inferior frontal junction	51	5	15	3.88	
	47	-3	14	3.59	
Picture-Word Interference: same>unrelated					
Left Angular [IPC/PGp] (39) and	-52	-68	36	7.80	1025
middle temporal gyrus (22)	-62	-40	40	4.52	
	-52	-60	22	4.10	
Right middle temporal (39) and	54	-50	18	5.83	1478
supra-marginal gyrus [IPC/PF] (40)	62	-38	38	5.47	
	58	-36	48	5.20	
Right superior frontal and medial gyrus (6/8)	16	44	50	5.62	197
	14	52	32	3.99	
	12	60	32	3.97	
conjunction $NSP \wedge PWI$ ($cong > neutral \wedge same > unrelated$)					
Right temporo-parietal junction [PGp, PFm]	41	-81	25	–	6
and inferior parietal lobe	55	-48	44	–	44
	53	-45	37	–	44

For the conjunction, inclusive masking of the two thresholded T-maps was performed. See also Figure 6.15 (white areas).

Figure 6.15: Results for conjunction of Numerical Stroop with Picture-Word Interference task.



Conjunction of $NSP : (congruent > neutral) \wedge PWI : (same > unrelated)$ NSP activity displayed in red, PWI activity in orange, areas mutually active in white. Neurological orientation (left = left). For corresponding MNI coordinates see table 6.7.

6.6 Discussion

For both paradigms, neural correlates for the conflicts in the Numerical Stroop task as well as the Picture-Word Interference task were mainly observed during the retrieval phase. During the response phase of the paradigms, significant results were only obtained for the Stroop effect of the PWI.

The *interference effect* of the Numerical Stroop task was reflected by activity in the right inferior temporal and lingual gyrus (BA 19), for the PWI, on the other hand, it was manifested in the left posterior middle temporal cortex and extending to the Angular Gyrus (BA 39).

Whereas no neural correlates for the *Stroop effect* were found for the numerical task, during the retrieval phase of the PWI a wide left hemispheric network was active in the inferior frontal and parietal lobe, which was inverted to the right hemisphere during the response phase.

Hence, during the retrieval phase, numerical conflicts were mainly processed in the right hemisphere, lexical conflicts, on the other hand, were primarily processed in the left hemisphere. The results lead to the assumption that the conflicts do not share neural substrates across task. Also conjunction analyses for the interference effect as well as the Stroop effect across the paradigms did not yield significant results.

The findings indicate that temporarily, the conflicts in both paradigms are processed primarily during the retrieval phase. Neurally, both paradigms show a vast difference in their underlying processes. First, they do not rely on common neural substrates and second, they are based in different hemispheres.

In both paradigms, neural correlates for the *reverse Stroop effect* (congruent>incongruent, same>related) (see Table 6.2 and 6.4) and the congruent>neutral and same>unrelated contrasts (see Table 6.7) were observed. As mentioned before, behaviourally, in both paradigms, responses were faster for the same condition (PWI) or identical condition (NSP) relative to the other conditions (for the behavioural results of the Numerical Stroop see Table 6.2, for the PWI see Table 6.7), accordingly, the four contrasts were expected to depict facilitation effects.

However, the reverse Stroop effect in the Numerical Stroop task was correlated with the BOLD signal in the right inferior frontal gyrus (IFG), including the inferior frontal junction (IFJ) and temporo-parietal regions (see Table 6.2) during the retrieval phase and interpreted to reflect a heightened cognitive demand.

The reverse Stroop effect in the PWI task, on the other hand was localised in the right inferior parietal and left Angular Gyrus (Table 6.4). To investigate joint activation for the reverse Stroop effect across paradigms, a conjunction analysis was performed, which did not yield a significant result.

Finally, for the congruent>neutral contrast in the Numerical Stroop (see Table 6.7) and same>unrelated contrast in the PWI (see Table 6.7) mutual activity on the junction of the right temporal, parietal and occipital lobe (TPJ) was detected. Activity in the right TPJ was observed for the reverse Stroop contrast in the Numerical Stroop task (see Paragraph 6.2 *Reverse Stroop effect* on p. 68).

When considering the results we have to keep in mind that the *congruent* and the *same* condition constituted an exception from the procedure for the unrelated or neutral condition: during the retrieval phase, target and distractor referred to the same lexeme and could be merged into one response. Therefore, during the response phase, the answer was presumably already prepared and the participant did

not have to make a choice.

There is evidence that the right TPJ is involved in the resolution of conflict, the detection of salient cues, for switching and dividing attention, in particular, when irrelevant objects must be ignored and the information has to be stored and maintained (Chang et al., 2013; Cieslik et al., 2015; Jakobs et al., 2012; Krall et al., 2014).

According to Cieslik et al. (2015, p. 30), "the right TPJ has been associated with predictive motor coding, including the updating of action expectations and the comparison of pre-prepared programs with current task requirements [..] as well as updating of temporal predictions of the onset of the next stimulus and its associated response".

Right TPJ activity was, for instance, observed in a meta-analytic connectivity modeling (MACM) analysis for variations of a manual two-choice reaction time task in which the neural correlates of increasing demands on sensorimotor top-down control were investigated (Jakobs et al., 2012). The authors conclude that "right TPJ may integrate 'collaterals' of sensory processing and apply (ensuing) contextual frames, most likely via modulation of preparatory loops" (Jakobs et al., 2012, p. 2389).

Mutual activity of the right TPJ in the identical and same condition may thus reflect the effort to retrieve identical lexemes from different sources and merge both into one response, whilst maintaining the resulting information until the cue is presented.

In the congruent trials of the Numerical Stroop task, additional activity in the right inferior frontal gyrus, in particular, activation of the inferior frontal junction was present, which was not observed in the PWI.

In the *same* trials of the PWI, on the other hand, left Angular Gyrus (AG) activity was detected, which was not observed during the Numerical Stroop task. Involvement of the left AG – including Wernickes area – in the PWI may indicate the use of verbal stimulus material as opposed to numbers (Binder et al., 2009). Lesions in the respective temporo-parietal area are reported to elicit deficits in semantic control (Noonan, Jefferies, Corbett, & Lambon Ralph, 2010; Jefferies & Lambon Ralph, 2006) and a reduced and delayed activation of thematic relations (Mirman & Graziano, 2012).

The findings suggest that the right temporo-parietal junction mediated the processing and integration of two redundant stimuli from different sources, independent from task or core system.

Chapter 7

General Discussion

The present study investigated the conflict between the target and the distractor in the Numerical Stroop task and in the Picture-Word Interference task. Two questions were addressed: First, does the cognitive conflict occur during the retrieval phase, when the stimulus is perceived and retrieved from memory, or is it located at the response phase, when the answer is prepared for articulation? Second, does the resolution of the conflict for number and object representations rely on common neural substrates?

In Stroop-like tasks, relatedness of two dimensions typically evokes a conflict between the relevant and the irrelevant response. On the other hand, if the relevant and the irrelevant response are identical, the performance is facilitated. Accordingly, the highest conflict was expected to be captured by comparing the related (or incongruent) to the identical condition (*Stroop effect*). By comparing the related to the unrelated condition or the incongruent to the neutral condition, I expected to capture the impact of the relatedness between target and distractor (*Interference effect*) in the Picture-Word Interference paradigm (PWI) and in the Numerical Stroop paradigm (NSP).

To locate the processing stage during which interference occurs, the retrieval phase and the response phase were segregated with a temporal delay. Longer reaction times in the delayed paradigm are interpreted to reflect an increased attentional demand during the *response phase*. Because the participant is expected to have ample time to retrieve the name of the target and the distractor, consequently the reaction time differences are interpreted to not reflect competition due to retrieval conflicts. In the immediate naming paradigm, technically speaking, again, response latencies are measured. However, with these response latencies, due to the close temporal proximity of the retrieval phase and the response phase and with only one behavioural measure, the source of the conflict cannot be located directly. Instead, by comparing the findings from both experiments, the locus must be deduced: if a conflict is *absent* in the delayed naming paradigm, but *present* in the immediate naming paradigm, we can derive the conclusion that a conflict occurred, but it was solved before the response was made, hence, it occurred during the retrieval phase.

The following predictions were made for the response latencies in the delayed naming task: If the interference effect arises at the retrieval phase, then the conflict should not be observed when participants delay their responses. However, if the interference originates at the response phase, then it should still be observed in the delayed naming task (Janssen et al., 2008).

I tested the predictions with an immediate as well as a delayed version of the Numerical Stroop task and the Picture-Word Interference task. In the immediate naming condition, the relevant and the irrelevant dimension appeared simultaneously, and participants were instructed to respond immediately. In the delayed naming condition, the stimuli were presented in the same manner, but the participants had to delay their responses until a cue was shown.

With only one behavioural measure, the source of the conflict cannot be located directly. As a consequence, I've been using a fMRI experiment which allowed me to separately model the BOLD response associated with retrieval and response selection. Sensitivity to the conflict should result in a monotonic relation between the relatedness and the BOLD signal, with the highest activation for the related condition and the least activation for the identical condition.

For the retrieval phase and the response phase, different assumptions were made:

During the retrieval phase, the challenge was that both, the target (picture/quantity) as well as the distractor word had to be retrieved, encoded and memorized. For the two cognitive core systems, different brain areas were expected to reflect the increased cognitive demand: For the Numerical Stroop task, I expected to see differences in the contrast between incongruent and neutral trials upon stimulus

presentation, if the conflict arises during the counting phase. Given previous findings (see Chapter 2.1 *Numbers* and 4.1.1 *Number Stroop*), the increased cognitive demand was expected to be correlated with the BOLD signal in the horizontal segment of the intraparietal sulci (hIPS) (e.g. Dehaene et al., 2003).

In the Picture-Word Interference task, I hypothesized that I would see differences in the contrast between related and unrelated stimuli contingent upon stimulus presentation, if the semantic interference effect is a lexical effect. Given the previous findings (see Chapter 2.2 *Objects* and 4.1.2 *Object Stroop*), I expected these effects to mainly arise in the left middle temporal gyrus (Indefrey, 2011) and inferior frontal gyrus (Price, 2012).

By contrast, if the interference effect is a response conflict, I expected to see a difference in activation between incongruent and neutral or related and unrelated stimuli contingent upon cue presentation, presumably in the anterior cingulate cortex (ACC) (Botvinick, 2007) and inferior frontal junction (Brass et al., 2005) in both tasks.

7.1 Behavioural Task Effects

As expected, the naming latency patterns in the Number Stroop task and the Picture-Word Interference task show a close resemblance, which is interpreted to indicate that conflicts in the number core system and in the object core system can be explained with a single cognitive process underlying both tasks.

In both paradigms in all immediate naming trials, a robust Stroop effect as well as an interference effect are observed. The results indicate that the irrelevant distractor word has indeed interfered with the naming of the target. The naming latencies are not only increased in the context of any irrelevant distractor word (Stroop effect), but also the relatedness of target and distractor does have an impact on the naming latencies (interference effect).

I conclude that during the related and incongruent trials of the Stroop paradigms the two cognitive representations, namely reading and counting or reading and picture naming were actually placed into competition.

The findings are in line with earlier investigations on the Counting Stroop task (e.g. Bush et al., 1998; Pagano & Mazza, 2013; for a review, see Chapter 4.1.1 *Number Stroop*) and they are also in line with previous results for conceptually related target-distractor pairs in the PWI (e.g. Schriefers et al., 1990; Damian & Bowers, 2003; for a review see Chapter 4.1.2 *Object Stroop*).

Interference Effect In both paradigms, reaction times were increased in the presence of a closely associated, but irrelevant word, but only when target and distractor were presented simultaneously. In the Picture-Word Interference paradigm, the interference effect was not significant at SOAs as short as +50 ms, i.e. with the word presented shortly after the picture (PWI, Exp. 1, Section 5.2). During the Numerical Stroop task, the incongruent number word interfered with the counting procedure, but only for immediate naming and not for delayed naming (NSP, Exp.1 and 2, see Section 5.1).

Therefore, I propose that in both paradigms, a cognitive conflict was actually present, but it was not observed when the response was delayed. The results indicate that interference had not occurred at the response stage.

Stroop Effect The Stroop effect is not only observed in all immediate naming experiments (NSP, Exp. 1, see Section 5.1, PWI with SOA=0; Exp. 1, Section 5.2), but, as expected, it is also present when the participants' response is postponed (SOA PWI, Exp. 1 and Exp. 2, Section 5.2 and NSP, Exp. 2).

The similar reaction time patterns for semantic and numerical conflicts support the notion that the Picture-Word Interference task and the Numerical Stroop task are two variants of the same paradigm (cf. MacLeod, 1991) and that both rely on the same cognitive process.

7.2 Functional Imaging Task Effects

Trying to tease apart effects of retrieval and response conflicts in two Stroop paradigms, I predicted two different activation patterns for the retrieval phase and one pattern for the response phase.

Regions that reflect the presence of a cognitive conflict were hypothesized to show the highest activation in the condition that yields the strongest conflict, namely the incongruent condition for the Numerical Stroop task and the related condition for the Picture-Word Interference task.

7.2.1 Interference Effect

The behavioural naming latency patterns in the Number Stroop task and the Picture-Word Interference task showed a close resemblance which was interpreted to indicate that conflicts in the number core system and in the object core systems can be explained with a single cognitive process underlying both tasks.

For the interference effect, in both paradigms, also the neural activation pattern resembles the one obtained with the reaction times: it was reflected by significant brain activity during the retrieval phase, which was not observed during the response phase. In the Numerical Stroop task, interference was correlated with activity in the right hemisphere, in particular, in the lingual gyrus. In the Picture-Word Interference task, however, the BOLD signal was correlated with activity in the left posterior MTG, extending to the Angular Gyrus. I conclude that the processing costs have occurred during the retrieval phase, i.e. early in the processing stream, for both - object and number representations -, but that they do not rely on common neural substrates.

Picture-Word Interference task During the retrieval phase of the Picture-Word Interference task the interference effect is indeed reflected by enhanced activity in the left MTG (see Table 6.4 and Figure 6.9). Hence, the neuronal pattern for the *interference effect* resembles the one obtained with the reaction times in the PWI. In the Picture-Word Interference task, neuronal activity as well as reaction times reflect semantic competition during the selection of target and distractor, but not during the response phase.

As mentioned in Chapter 4.1.2 *Object Stroop*, activity of the left MTG has been observed in the Picture-Word Interference task in the context of categorical distractors (De Zubicaray et al., 2001; Schnur et al., 2009). However, previous studies have observed pronounced activity of the left MTG in the context of picture-distractor combinations which actually facilitate picture naming (Abel et al., 2012; Schnur et al., 2009; Muehlhaus et al., 2014).

Also in the present study, the left MTG and Angular Gyrus were not only found active for the related condition, but also for the same condition (see Table 6.6). Hence, contrary to expectations, the left posterior MTG was not solely responsive to semantic interference -, but also to semantic facilitation effects. A possible interpretation is that the left MTG and left Angular Gyrus may be responsive to the resolution of close semantic proximity between the picture and the distractor word: In the related condition, the picture and the distractor were part of the same semantic category, in the identical condition, they referred to the same lexeme.

This assumption is supported by the finding that the left Angular Gyrus, which was found active for the 'semantic proximity' conjunction (i.e. $rel > unrelated \wedge same > unrelated$) as well as for the 'same' conjunction ($same > rel \wedge same > unrelated$) is considered to play a crucial role in semantic processing, and assumed to occupy "a position at the top of a processing hierarchy underlying concept retrieval and conceptual integration" (Binder et al., 2009, p. 2776) (cf. Chapter 3 *Word production*). The left Angular Gyrus is also proposed to play a crucial role in semantic processing as opposed to perceptual processing (Seghier, Fagan, & Price, 2010).

However, the fact that both – the same as well as the related condition – reflect a close semantic relatedness between target and distractor does not explain the large behavioural reaction time difference between the conditions, namely the observed facilitation effect for the same condition and the interference effect for the related condition. However, assuming that both conditions rely on initial priming effects, this contradiction can be resolved:

For instance, according to Abdel Rahman and Melinger (2009), semantically related distractor words generally facilitate the retrieval of a concept; only if the lexical cohort is large enough, lexical competition actually outweighs conceptual facilitation and, as a consequence, interference effects emerge. This would mean that in the present case, picture naming in the same and the related condition was initially facilitated, resulting in a similar neural activation pattern. Subsequently, only in the related condition a lexical cohort was activated, and as a consequence, the initial facilitation effect was outweighed by the interference effect, which was observed behaviourally.

Finkbeiner and Caramazza (2006) drew a similar conclusion from a masked and a visible version of the Picture-Word Interference task. In both versions, semantically related and unrelated distractor words were presented shortly before the picture, but in the masked priming condition the distractor word was preceded and followed by strings of symbols or letters. The authors report that related trials in the masked priming condition led to semantic facilitation effects, whereas related trials in the visible condition interfered with picture naming. According to the authors, in the visible condition a phonologically well-formed response of the distractor word is formulated. This response interferes with target naming.

However, in the masked condition, the formulation of the well-formed response is prevented, leading to facilitation effects. Hence, according to the interpretation of Finkbeiner and Caramazza (2006), facilitation effects precede interference effects, but different to Abdel Rahman and Melinger (2009), facilitation is not attributed to the conceptual stage but to the lexical selection phase, and interference effects are interpreted to occur during the response phase.

In any case, activity in the left MTG and Angular Gyrus could be interpreted to reflect underlying facilitation effects in the related and the same condition, which were caused by priming effects due to the semantic proximity between target and distractor.

Numerical Stroop During the retrieval phase of the Numerical Stroop task, the interference effect was correlated with the BOLD signal in the right inferior temporal gyrus (see Table 6.2, Figure 6.5).

Pronounced activity in the right inferior temporal and lingual gyrus is interpreted to reflect a high attentional load, in particular for the processing of global as compared to local aspects of hierarchically organized visual stimuli (Fink et al., 1996), especially when combined with a high working memory load (Pessoa & Ungerleider, 2004).

The finding indicates that the retrieval and encoding of two incongruent number stimuli (incongruent condition) indeed elicited a higher attentional demand than the retrieval and storage of a number stimulus and a common noun (neutral condition). However, contrary to expectations, the conflict was not located in the intraparietal sulcus, indicating that the conflict was not actually a numerical conflict, but eventually rather reflecting a high attentional load.

Therefore, the neuronal pattern for the interference effect resembles the one obtained for the reaction times in the Numerical Stroop task: Reaction times are increased for the incongruent compared to the neutral condition in the immediate naming experiment, i.e. reflecting interference effects. Delaying the response had eliminated the interference effect in the naming latencies. To sum up, in the Numerical Stroop task, neuronal activity as well as reaction times reflect competition during the selection of target and distractor, but not during the response phase.

7.2.2 Stroop Effect

Behaviourally, robust Stroop effects were obtained during the retrieval phase and the response phase for the Numerical Stroop task as well as for the Picture-Word Interference task. However, the neural activation pattern for the Stroop effect was ambiguous: In the Picture-Word Interference task, the activation pattern for the Stroop effect indeed resembled the one obtained with the reaction times, consequently, the Stroop conflict was attributed to the retrieval as well as the response phase.

In the Numerical Stroop task, the neural activation pattern for the Stroop effect suggest an inverse relation: during the retrieval phase, the congruent – but not the incongruent – condition evoked a strong neural response at the retrieval stage which seems to be solved before the response stage is reached. However, at the response stage, the significant reaction time difference between the incongruent and the congruent condition is not reflected by neuronal correlates.

Picture-Word Interference Task As expected, the Stroop effect is correlated with the BOLD signal in the left inferior frontal gyrus (see Figure 6.10). In addition, activity of the left inferior frontal junction (IFJ) is observed. As a result, during the retrieval phase a large fronto-parietal network in the left hemisphere, including the inferior frontal, inferior and superior parietal lobe, the DMPFC and SMA, is interpreted to indicate a strong lexical conflict and an increased cognitive and working memory demand elicited by the retrieval of two lexical items (Indefrey & Levelt, 2004; Binder et al., 2009). During the response phase, a smaller fronto-parietal network in the right hemispheric is assumed to reflect a response conflict (Cieslik et al., 2015). Therefore, neuronal activity as well as reaction times indicate the presence of a Stroop conflict due to the selection of the picture name and the distractor word and due to a response conflict.

Hence, for the Picture-Word Interference task, the neuronal pattern of the Stroop effect resembles the one obtained with the reaction times in the PWI: Behavioural results as well as neural activation patterns suggest that the response phase contributes to the Stroop conflict. Furthermore, the neural activation pattern supports the assumption that a strong Stroop conflict also occurred during the retrieval phase.

Contrary to expectations, the inferior frontal junction does not reflect response conflicts, but it is found active during the retrieval phase. Recently, the IFJ has been suggested to be involved in the initiation of visual short term memory representations (Sneve, Magnussen, Alnæs, Endestad, & D'Esposito, 2013, cf. Paragraph 7.3.2).

Numerical Stroop The behavioural reaction time patterns for the Stroop effect in the delayed naming paradigm reflect an increased attentional demand during the response phase, which is suggested to be caused by selecting one of two items (incongruent condition) versus responding one item (identical condition). However, surprisingly, for the response phase of the Stroop contrast in the Numerical Stroop task, no significant brain activity was detected. Also during the retrieval phase, the Stroop contrast and the BOLD signal are not significantly correlated.

Instead, the Reverse Stroop effect (congruent > incongruent condition) did yield significant neural activity changes in a right fronto-parietal network, comprising the inferior frontal gyrus (IFG), inferior frontal junction (IFJ) and temporo-parietal junction (TPJ). The involvement of the right IFJ in retrieval, but not response conflicts, with the highest activation during the congruent trials was further illustrated by the Percent Signal Change graph (see Figure 6.6). These brain regions are typically interpreted to reflect an increased cognitive demand (Cieslik et al., 2015; Krall et al., 2014).

The demand in the congruent condition may be interpreted to be driven by the participants' attempt to align the magnitude of the quantity and the number word and to decide whether they are off balance. In other words, participants' were presumably struggling to disentangle the magnitude of the quantity and the number word and to integrate both into one response.

However, in a study by Hedden and Gabrieli (2010) with Navon figures, activity in the right inferior frontal gyrus was also obtained for the congruent condition and interpreted to indicate facilitation effects. In their study, also incongruent and neutral Navon figures were presented. Congruent letters were composed of either H or S on local and global levels, incongruent stimuli contained incompatible letters on both levels (e.g., global letter 'H', composed of 'S') and neutral stimuli contained an O, which was never associated with a response. Participants had to name either the global letter or its local parts. As mentioned before, activity of the right inferior frontal gyrus, including BA 44, was observed for the congruent condition. Consequently, the authors conclude that "[t]his result is not compatible with an interpretation that right VLPFC is selective to inhibitory control, and instead suggests that VLPFC may be engaged whenever multiple information channels contain potentially relevant information that must be selected for continued processing" (Hedden & Gabrieli, 2010, p. 10). However, it must be noted that in the study by Hedden and Gabrieli (2010), the congruent condition was contrasted with the neutral condition, in which the distractor was not response-relevant. Even if each stimulus dimension – namely the target and the distractor – represented a potentially relevant information channel, in the present study the channels in the congruent and the incongruent condition contained relevant information. Consequently, Hedden and Gabrieli's interpretation cannot be derived to explain the results of the Reverse Stroop contrast.

The horizontal segment of the intraparietal sulcus (hIPS), or, more specifically, the left superior and inferior parietal lobe, including hIP3, was actually involved in the counting process of the Numerical Stroop task (see task network in Table 6.1 and 6.4), but apparently the hIPS was not responsive to the numerical conflict, in other words, it was neither correlated with the Interference nor with the Stroop effect in the Numerical Stroop paradigm (see Table 6.2).

In conclusion, in the Numerical Stroop task, for the interference effect, the neuronal pattern resembles the one obtained for the reaction times. Accordingly, the behavioural as well as the neural results provide evidence for the assumption that interference effects occur during the counting phase.

Regarding the Stroop contrast in the Numerical Stroop task, the strong behavioural effect was not reflected by neuronal substrates. Hence, the assumption that the Stroop effect might elicit conflicts during the retrieval and the response phase is not reflected by a neural activation pattern. Instead, it provides evidence for the hypothesis that a higher processing demand may have actually occurred during the retrieval phase of the congruent condition and that the effort was completed before the participants' attempt to respond.

Taken together, the findings for the Stroop effect suggest that actually the congruent condition elicited a higher processing demand during the retrieval phase. Because for the congruent condition, the reaction times are speeded at the response stage, the conflict is interpreted to be actually solved during the retrieval phase.

Conclusion The following conclusions can be derived from the findings: First, behavioural reaction time data as well as neural activation patterns support previous assumptions regarding the locus of the interference effect in both paradigms; consequently, conflicts in the Picture-Word Interference task and the Numerical Stroop task seem to be resolved during the retrieval stage.

Second, for the Stroop effect, the behavioural and neural activation patterns show a close resemblance for the Picture-Word Interference task, but not for the Numerical Stroop task: As predicted from the be-

havioural data in the Picture-Word Interference task, also the neural activation implies a strong response conflict. Furthermore, neural activation indicates that the conflict also seems to be present during the retrieval phase.

In the Numerical Stroop task, however, behavioural and neural activation patterns for the Stroop effect suggest a more complex relation. The findings indicate that during the retrieval phase, the congruent condition was actually more demanding than the incongruent condition, however, during the response phase, behavioural reaction time data suggest that the problem was solved and the response was prepared.

Third, the resolution of numerical and lexical conflicts does not seem to rely on common neural substrates. For the Picture-Word Interference paradigm, the interference effect correlated with the left MTG, the Stroop effect was reflected by a fronto-parietal network with a left hemispheric dominance during the retrieval phase and a right hemispheric dominance during the response phase.

In the Numerical Stroop task, the interference effect is correlated with the right lingual gyrus. The Reverse Stroop effect was reflected by right inferior frontal and occipito-parietal activity during the retrieval phase.

Accordingly, the findings support the notion that the number core system and the object core system follow different pathways, and that they may be seen as separate systems. The findings support the assumption that both systems actually are domain-specific, encapsulated and isolated (Spelke, 2003).

Fourth and finally, neural findings suggest that the congruent (NSP) and same condition (PWI) rely on different cognitive processes. Initially, a strong conflict was expected to occur in the incongruent (NSP) and the related (PWI) condition, by contrast, in the congruent and same condition the task was expected to be facilitated. Hence, in the Picture-Word Interference task, the neural results for the same condition are indeed interpreted to reflect facilitation effects. However, in the Numerical Stroop task, neural findings for the congruent condition contradict this assumption. Even if the behavioural reaction time patterns indicated that the congruent condition facilitated the *response procedure*, the neural activation pattern indicates that the *counting procedure* was actually exacerbated.

To begin with, as predicted, it was demonstrated with the Picture-Word Interference task (Table 6.4 and Figure 6.9), that the left posterior temporal gyrus was responsive to interference effects. However, the same portion of the left temporal and Angular Gyrus was also active when the picture name and the distractor word were identical (same condition). It was therefore concluded that the left Angular Gyrus may provide a neural substrate for basic underlying facilitation effects.

For the Numerical Stroop task, a right fronto-parietal network, which is interpreted to reflect inhibitory processes in cognitive control tasks (Cieslik et al., 2015; Kim et al., 2011; Sundermann & Pfleiderer, 2012), was found active during the congruent condition, but not during the incongruent condition. The findings were interpreted to reflect the participants' struggle to align the magnitude of the quantity and the number word and to decide whether they are off balance.

Even if the same condition in the PWI is interpreted to reflect facilitatory processes and the congruent condition in the NSP is assumed to indicate inhibitory processes, both share a common neural substrate, which is based in the parietal lobe (see Table 6.7).

The finding may seem contradictory, as facilitation is typically viewed as an behavioural inverse of inhibitory processes. Hence, facilitation effects are expected to involve reduced activations relative to baseline in regions which reflect inhibition. However, in the study by Cohen Kadosh, Cohen Kadosh, Henik, and Linden (2008), the bilateral posterior IPS was activated for both interference and facilitation. The authors conclude that both effects might not be completely independent mechanisms, and that they are both partly subserved by shared brain areas in the parietal and frontal cortices (Cohen Kadosh et al., 2008, p. 7878).

Consequently, in the present study, activity in the right parietal lobe and temporo-parietal junction, which was found active for the congruent condition in the NSP as well as the identical condition in the PWI (see Table 6.7) is interpreted to subserve facilitation and interference effects. It is suggested to reflect the integration of two identical lexemes from different sources into one response. The right TPJ is typically interpreted to modulate the integration of conflicting information (Jakobs et al., 2012) and reflect attentional engagement (Corbetta & Shulman, 2002; Vetter, Butterworth, & Bahrami, 2011).

Moreover, as mentioned in chapter 2.1.2 *subitization*, the 'number core system 1' for small and exact quantities (see Chapter 2.1) is suggested to operate via the same system as object recognition (see Chapter 2.2) Cutini et al. (2014); Vuokko et al. (2013). Particularly, pronounced activity in the right TPJ is often observed for the enumeration of small amounts of numbers (Dehaene, Posner, & Tucker, 1994; Hyde & Spelke, 2011). Furthermore, the right occipito-temporal cortex is assumed to be a part of the ventral visual stream (Vuokko et al., 2013) and to play a crucial role in object recognition (Di Russo et al., 2002; Schendan & Lucia, 2010). Consequently, Chesney and Haladjian (2011) and Vuokko et al. (2013) have

suggested, that the enumeration of a small set of items and the so-called Object Tracking System may indeed utilize the same underlying visual mechanism, which might eventually be based in the right TPJ (Piazza & Izard, 2009; Vuokko et al., 2013).

In particular, Jakobs et al. (2012, p. 2389) concluded from a multi-study conjunction that the "right TPJ may represent a key region for the integration of sensory stimuli and contextual frames in action control". In the present task, this would mean that the right TPJ was involved or maybe even crucial for the integration of the stimulus and its context – i.e. the distractor – into one articulatory movement, namely the response.

However, one could argue that the activation produced in the congruent condition in the Number Stroop task (NSP) and the identical condition in the Picture-Word Interference task (PWI) could be attributed to novelty effects, since congruent and identical trials were presented infrequently in both tasks (20% of the stimuli)[1]. However, novelty effects are typically observed for salient stimuli, for instance, for infrequent pictures of objects among a stream of triangles (Wessel, Danielmeier, Morton, & Ullsperger, 2012) or bright, colourful and complex fractal pictures compared to circled dots (Gur et al., 2007). In the present study in both paradigms the target and the distractor appeared in exactly the same manner across conditions, i.e. in the NSP a row of number words was presented and in the PWI a picture and a word were displayed. Hence, only the meaning of the word was manipulated, and not the appearance of the stimuli. Furthermore, the frequency of novel stimuli compared to standard stimuli is typically lower than 20%, i.e. for instance 9% (Strobel et al., 2008), 13% (Wessel et al., 2012) to 15% (Gur et al., 2007). It is therefore unlikely that the effects can be attributed to surprise or novelty effects.

7.2.3 Neural Correlates of Response Conflicts

Upon cue presentation the anterior cingulate cortex (ACC) (Botvinick, 2007) and inferior frontal junction (Brass et al., 2005) were hypothesized to picture response conflicts. As mentioned earlier, in the present study activity in the inferior frontal junction (IFJ) was actually observed during the retrieval phase but not during the response phase. Contrary to expectations, also the cingulate cortex was not sensitive to response conflicts; it was observed neither for the interference nor for the Stroop contrast in any of the paradigms. However, activity of the middle and anterior cingulate cortices (ACC) was present during the task phase and the response phase of the PWI (see Table 6.3 and Figure 6.8) and also during the counting phase of the NSP (see Table 6.1 and Figure 6.4).

This finding is unexpected, but not unprecedented: a similar observation was made by Zysset, Müller, Lohmann, and von Cramon (2001) with fMRI on the Colour-Stroop task. The authors state "that the ACC is not specifically involved in interference processes. The ACC seems rather responsive to motor preparation processes [...]. We argue that the region around the banks of the inferior frontal sulcus is required to solve interference problems, a concept which can also be seen as a component of task set management" (Zysset et al., 2001, p. 29). In line with this assumption, Matsumoto and Tanaka (2004) have suggested that the ACC and the lateral prefrontal cortex (LPFC) may act jointly. According to them, the ACC is assumed to detect 'conflicts between plans of actions'. Following this, in particular when such a conflict is detected, the ACC is assumed to recruit greater cognitive control in the LPFC (Botvinick et al., 2001; Matsumoto & Tanaka, 2004). Applied to the present task, we may assume that the ACC was indeed responsive to the task requirement in all conditions, subsequently, according to the particular cognitive demand of each condition, frontal cortices were recruited. Lateral prefrontal cortices were, for example, found active in all stages of the Stroop contrasts in the PWI (Table 6.4, 6.5 and 6.6) and in the Reverse Stroop contrast of the NSP (Table 6.2).

7.3 Further Remarks

Having discussed the two effects of main interest in the current study, I will proceed to some additional findings. First, the IPL, and in particular the hIPS, was assumed to be involved in numerical processing and expected to be sensitive to conflicts in the Numerical Stroop paradigm. However, the present results suggest that the role of the hIPS is not specified to the processing of numbers, but must be considered more general. This assumption will be discussed in the following section.

Second, because participants were forced to memorize the target as well as the distractor until the colour of the cue was known, both responses had to be prepared and upon cue presentation, one them had to be chosen. Therefore, the impact of feasible short-term memory components will be discussed

[1] For the statistical analysis, in both paradigms, the number of observation was adjusted.

subsequently. Because the cue also indicated to alternate between target naming and distractor naming, also task-switching effects will be addressed.

Third, the Numerical Stroop task provided us with the opportunity to quantify the proximity between the target quantity and the distractor, therefore I'll close the discussion with some remarks on the numerical distance effect and subitization.

7.3.1 The Inferior Parietal Lobe: Processing Small Numbers of Objects?

In Chapter 2.1 on the processing of numbers, the inferior parietal lobe (IPL), and, in particular, the intraparietal sulcus (IPS), has been suggested to host a module for the number sense (e.g. Dehaene, 2011). However, in Chapter 2.2 on the processing of object perception and recognition, the IPL was suggested to be part of the dorsal visual stream and to play a crucial role in the processing of spatial features in object perception. This suggests that the role of the inferior parietal sulcus cannot be specified to the processing of numbers but must be considered more general.

To begin with, in the present study, the Picture-Word Interference task showed significant activation of the inferior parietal lobe and also the IPS during the retrieval phase (see task network, Table 6.3) and also for the Stroop contrast (Table 6.4). During the retrieval phase of the PWI, the picture was perceived and its label was retrieved. During this phase, not only left intraparietal activity, but also pronounced bilateral inferior temporal and ventrolateral prefrontal (VLPFC) activity is observed (see Table 6.3 and 6.8). In the left hemisphere the task network comprises middle temporal activity, extending to the left temporal pole. In both hemispheres, the superior temporal cortices are activated.

As mentioned in Chapter 2.2 on the processing of objects, these regions are supposed to be part of the dorsal and the ventral visual stream and assumed to play a vital role in object recognition: First, the dorsal visual stream, comprising parietal regions, is suggested to support attentional processes and the integration of spatial features in visual information (Treisman, 1998; Zachariou et al., 2015). The ventral stream, comprising inferior temporal cortices, is proposed to play a crucial role in object recognition (DiCarlo et al., 2012). More particular, Clarke et al. (2012) and DiCarlo et al. (2012) have suggested a specificity of semantic processing in a posterior-to-anterior gradient along the left temporal lobe, with an increasing fine-grained semantic analysis projecting to more anterior regions. Hence, the anterior ventral part of the left temporal lobe is assumed to contribute to the conceptual processing of complex visual information, with anterior structures contributing more to the representation of semantic conceptual associations (Bonner & Price, 2013; Peelen & Caramazza, 2012).

Accordingly, as suggested by Bonner and Price (2013, p. 4213), the left ventral temporal pole may have contributed to decoding information about the abstract conceptual properties of the picture by incorporating a broad framework based on perception and semantic memory. In collaboration with the temporal lobe, the VLPFC may have guided the top-down retrieval of knowledge from long-term memory and the selection of the target item among its competitors (Badre et al., 2005).

However, during the retrieval phase, the participants did not only have to retrieve and memorize the meaning of the picture and the word, but also their respective source and to store both separately. This implies that the participants had to retrieve the picture name and the word, i.e. 'what', and also the corresponding origin, i.e 'where'. In other words, this particular task also provided a spatial requirement, presumably with a high attentional demand.

The finding converges well with an assumption by Cusack, Mitchell, and Duncan (2009), suggesting that the inferior IPS may hold 'tokens' or 'tags' which are required whenever multiple items are represented simultaneously.

Consequently, as previously mentioned in the chapter on the processing of numbers (Chapter 2.1), Friedrich and Friederici (2013, p. 8) have proposed to reconcile the diverging and contradictory findings regarding the inferior parietal sulcus on numerical processing. Accordingly, they assume that the intraparietal sulcus may process a small number of objects, representing a simple form of structured information, which is made available for prefrontal regions.

This assumption is also fully compatible with the findings from the Numerical Stroop task. Also in this task, multiple items had to be maintained simultaneously. Accordingly, activity of the left intraparietal sulcus in the task network of the Numerical task does not necessarily reflect numerical processing (see Table 6.1 and Figure 6.4).

Furthermore, the pattern of activation in the task network of the Picture-Word Interference task as well as of the Numerical Stroop task strikingly follow the 'fronto-parietal control system' (FPCS) as suggested by Vincent, Kahn, Snyder, Raichle, and Buckner (2008). Also for the Stroop contrast in the Picture-Word Interference task corresponding regions were found active. The FPCS includes the inferior

parietal lobe, anterior cingulate cortex, lateral prefrontal cortex (LPFC) and anterior insula. According to Vincent et al. (2008), the FPCS is typically engaged by tasks that require a controlled processing of information, especially if multiple interdependent contingencies must be maintained simultaneously, requiring support by the working memory and attentional resources. In addition, the FPCS is supposed to "show sustained activity over the duration of a task block [...], which may be related to a requirement for integration of information throughout the block, or the sustained maintenance of the task set" (Vincent et al., 2008, p. 3337).

The FPCS converges well with the findings regarding meta-analyses on cognitive control, including Stroop tasks, but also go/no-go tasks, stimulus-response compatibility, Flanker, Simon, antisacchade and stop-signal tasks. In particular, consistent across-study activation is reported in the inferior parietal lobe, prefrontal cortex, anterior insula and anterior cingulate cortex (Cieslik et al., 2015; Levy & Wagner, 2011; Nee, Wager, & Jonides, 2007).

7.3.2 How do working-memory components contribute to the results?

While perceiving and processing the experimental stimuli, the participants did not know whether they would have to respond with the target or the distractor. Therefore in all but the identical trials the participants had to memorize the target as well as the distractor and postpone their response until the cue was shown. Hence, one might argue that the study also contained a working memory component. As might be reasonably expected, working memory (WM) should mostly affect the conflicting trials during the retrieval phase in which two items had to be retrieved and stored.

According to Bledowski, Rahm, and Rowe (2009, p. 13739), "[w]orking memory supports many higher cognitive functions by keeping a small number of items available in a state of active neural representation, and by selecting and attending preferentially to that item that is momentarily most relevant". Arguably, working memory is a central component of higher cognitive functions such as intrusion resistance, distractor resistance, updating and shifting (Nee et al., 2013). With that said, it is not surprising that the VLPFC and the DLPFC – which are typically found active in cognitive control task – are considered to play a prominent role in networks supporting cognitive control of *memory* (Badre et al., 2005; Badre, Lebrecht, Pagliaccio, Long, & Scimeca, 2014).

It seems unlikely, however, that working memory functions entirely explain the Stroop results in both paradigms.

For instance, as discussed in Chapter 2.1 on *Numerical Cognition*, activity in the dorsolateral prefrontal cortex (BA 9, 10, 46) was suggested to reflect a heightened working memory demand in numerical processing (Arsalidou & Taylor, 2011; Chochon et al., 1999). Actually, in the present study, during the counting phase of the Numerical Stroop task activity in the DLPFC (BA 8, 9, 10, 46) was not observed, hence, regions that are supposed to reflect higher working memory demands in numerical processing were not detected. However, a portion of the right VLPFC, namely the right inferior frontal gyrus (BA 44), was found active for the Reverse Stroop contrast (i.e. congruent>incongruent contrast, see Table 6.2, Figure 6.5). According to Nee et al. (2013, p. 277) "[t]he right IFG has been strongly implicated in the inhibition of prepotent responses" and it is associated with executive processes of working memory due to intrusion resistance. However, in contrast to the left IFG, the right IFG is only weakly associated with working memory functions. This assumption fits with the observation that the right IFG was found active for the congruent condition, in which the working memory load was supposed to be low. It thus seems unlikely that working memory demands played a crucial role in the processing of the Numerical Stroop task.

On the other hand, during the Picture-Word Interference task, some of the frontal areas which were active during the retrieval phase (see task network Table 6.3) are also associated with short-term and long-term memory functions. For example, as mentioned in Chapter 2.2.3, during object recognition, activity of the right VLPFC is interpreted to provide long-memory functions which facilitate recognizing familiar objects (Akirav & Maroun, 2006).

Also the inferior frontal junction has recently been suggested to play a central role in the initiation of short term memory representations. According to Sneve et al. (2013), the inferior frontal junction (IFJ) is preferentially involved in the encoding phase of visual short term memory (VSTM) functions, whereas the frontal eye field (FEF; BA 6) and the anterior intraparietal sulcus (aIPS) are assumed to support VSTM maintenance. The authors therefore suggest that the "IFJ exercises top-down control over perceptual areas to promote the successful establishment of task-relevant representations, perhaps by modulating feature processing" (Sneve et al., 2013). This assumption is in line with the findings from the present study, that is to say that the IFJ was not found active during the response phase, in which

STM representations had to be maintained, but during the retrieval phase, in which they were initiated (cf. Percent Signal Change graph 6.6 and 6.13).

Language-related working memory functions are associated with the left inferior frontal gyrus (LIFG) (Makuuchi et al., 2009; Makuuchi & Friederici, 2013). The left IFG is considered to play a crucial role in verbal working memory functions, and it is assumed to "perform a general executive function for verbal content" (Nee et al., 2013, p. 265). It was part of the task network in the Picture-Word Interference task and also found active during the retrieval phase of the Stroop contrast(Table 6.4). However, it also seems to be involved in selecting competing lexical alternatives from semantic memory (Thompson-Schill et al., 1997).

Keeping in mind that cognitive control processes are multi-faceted and extremely complex, it becomes apparent why a great deal of research is still aiming to understand the component processes of cognitive control and to delineate the functional organization of the corresponding neural network involved.

However, even if working memory functions did play a role in the Stroop tasks, it seems unlikely that they entirely explain the results regarding the conflicts.

task-switching In the present study, the participants had to postpone their response until the colour of the cue was known. Hence, because in some cases, the distractor represented an actual target, consequently, both the target and the distractor had to be prepared. At the response phase, the participants needed to switch between naming the target and the word. The task-switching component may be seen as an additional cognitive process, making the response phase more demanding than the retrieval phase. Also, compared to standard Stroop paradigms and Picture-Word Interference paradigms, in which the distractor can completely be ignored, in the present study, the relevance of the distractor was highly increased.

Hence, both the increased relevance of the distractor as well as the task-switching component might have strengthened the need to prepare production-ready responses during the retrieval phase (cf. Mädebach et al., 2011). Accordingly, in this case, one would expect an additional cognitive demand during the response phase and thus a strong neural response upon cue presentation. Hence, in the Numerical Stroop task, in which the experimental trials and the filler trials were nearly equally frequent (i.e. 57% of the trials were presented with a blue cue), in the incongruent and the neutral condition the distractor words were highly relevant and at the response phase the participants were forced to switch between the prepared quantity and the distractor word. Consequently, one would have expected a strong cognitive demand during the response phase. However, for these conditions during the response phase no neural correlates were obtained.

In the Picture-Word Interference task, on the other hand, the filler trials, which indicated to name the distractor, were less frequent (25% of the trials). Therefore, the participants were expected to focus more on preparing the picture name. Accordingly, compared to the frequent experimental trials a stronger task-switch effect would have been expected to emerge for the infrequent filler trials, which were not analysed in the present study. However, to complete the task successfully, also in this task, the distractor could not completely be ignored. Therefore, it cannot be ruled out that a task-switching component might have contributed to the results of the response phase for the Stroop effect in the PWI, but it is unlikely that task-switching effects were strong and that they entirely explain the results.

7.3.3 Numerical distance and subitization in the Numerical Stroop task

Using number stimuli in the Number Stroop task was expected to have two advantages. With the numerical distance between target and distractor, I assumed to be able to quantify the proximity between the target and the distractor. With this measure, I was hoping to be able to systematically investigate the impact of the numerical proximity. In line with previous findings regarding the numerical distance effect (Moyer & Landauer, 1967, cf. Chapter 2.1 Numbers), I hypothesized that the conflict would be stronger for close distances (e.g. target '1', distractor '2') compared to far distances (e.g. target '1', distractor '6'). Consequently, reaction times were expected to decrease for far distances. Second, neurally, sensitivity to the numerical distance effect was expected to result in an inverse monotonic relation between the distance and the BOLD signal, with the highest activation for the close distances and the least activation for the far distances.

However, contrary to expectations, in the present study, a numerical distance effect was neither reflected by the reaction time pattern nor by neural substrates.

Only in the immediate naming paradigm, the numerical distance effect was marginally significant (see Table and Figure 5.2 on p. 48). The behavioural reaction time pattern indicates that the reaction

times were indeed increased for the closest distance, i.e. one, but speeding up drastically beyond one. Consequently, the reaction time pattern indicates that actually a very close distance interferes more than farer distances, perhaps following a hyperbolic function (cf. Figure 5.2), but this question is yet to be clarified. However, contrary to expectations, the reaction times do not show a significant *linear* decrease.

This finding is unexpected and, at first sight, it might seem odd because supposedly the effect is pretty robust: As mentioned in Chapter 2.1 *Numbers*, it is observed for numerical judgements, for instance, when the magnitude of two digits must be compared (Moyer & Landauer, 1967) and also in the context of the number-size congruity paradigm, in which the magnitude of digits must be compared and the physical size must be ignored (Ansari et al., 2006; Kaufmann et al., 2005; Pinel et al., 2004). However, to my knowledge, it has not been mentioned in a Counting Stroop task yet (Bush et al., 1998, 1999; Venkatraman, Rosati, Taren, & Huettel, 2009). It might well be, as suggested by (Fias et al., 2001) and (Wong & Szűcs, 2013) that numbers do not automatically activate their numerical code (see Chapter 2.1 and 4.1.1). In this case, the numerical distance effect would presumably be dependent on a deep processing of the magnitude, and thus only present when the magnitude of the number is indeed crucial for solving the task. This is generally true for magnitude comparisons, but not applicable for the present study.

Finally, contrary to expectations, no neural correlates for the numerical distance effect were obtained. Although this finding is unexpected, it is not unprecedented: as mentioned in Chapter 4.1.1 *Number Stroop*, the numerical distance effect was not observed with the number-size congruity paradigm by Tang et al. (2006) and it was detected solely when close distances were compared to far distances or vice versa (Ansari et al., 2006; Kaufmann et al., 2005).

The fact that the comparison of extreme distances did yield significant results agrees with the previous assumption based on the reaction time pattern of the immediate naming paradigm, in which only the closest distance seems to have yielded longer reaction times.

subitizing Intuitively, the more items you have to count, the longer it should take. In other words: with increasing item quantity, reaction times are expected to be increased. However, enumerating one, two or three items is fast but starts slowing down drastically beyond four. At the same point, errors begin to accumulate (Trick & Pylyshyn, 1994). The numbers of one to three seem to be recognizable at a glance, which is called *subitization* (e.g. Dehaene, 2011).

These observations are in line with the findings from the present study: in the immediate naming task the reaction times were found to increase with quantity (see Figure 5.5a, p. 50). However, for one to three items, the reaction times did not differ, but they were slowing down rapidly for four to six items (see Chapter 5.1, Exp. 1, pp. 45).

In the delayed naming experiment, furthermore, reaction times were not increasing with quantity (Figure 5.5b), suggesting that, upon cue presentation, the counting process had indeed been completed and the response had been prepared (see Chapter 5.1, Exp. 2).

For the Numerical Stroop task, two conclusions can be drawn from these findings: First, the results indicate that the participants did not solve the task by memorizing a mental image of the stimulus and thus, by postponing the retrieval process to the response stage. Consequently, there is reason to believe that the retrieval phase and the response phase in the Numerical Stroop paradigm were indeed successfully teased apart with the delayed naming experiment.

Second, also in the present experiment, in accordance with previous findings (Trick & Pylyshyn, 1994; Dehaene, 2011), three number words were subitized. Even though the participants had to count words, which were, technically speaking, rather complex, apparently, three of them could still be perceived at a glance. Presumably, the reason for this was, that the words were ordered in a column. A canonical order is known to facilitate subitization (Piazza et al., 2002).

Because about half of the items were subitized and half were counted, both processes contributed to the task to the same extent.

As discussed in chapter 2.1.2, the brain areas for subitizing and counting both seem to rely on similar neural circuits; both seem to recruit the bilateral intraparietal cortices, but counting is assumed to have a stronger impact and it might additionally involve frontal regions (Cutini et al., 2014; Vuokko et al., 2013). Therefore, the neural circuits for subitizing and counting were not expected to differ.

7.4 Outlook

I have hypothesized that the processing costs for the Numerical Stroop task and the Picture-Word Interference task occur during the retrieval phase. Because brain areas which are supposed to be involved in

cognitive conflicts were indeed significantly correlated with the conflicting conditions during the retrieval stage, it was concluded that the conflict had most likely occurred early in the processing stream. Because during the response phase hardly any neural result was obtained, the question what happened during the response stage remains uncertain.

Especially the lacking results during the response phase of the Numerical Stroop contrast are intriguing, because behaviourally, large difference between the incongruent (or neutral) condition and the congruent condition had been obtained. Hence, the null results for the Numerical Stroop task are difficult to account for.

One hypothesis is that during the response phase, the facilitation effect of the congruent condition was indeed higher than the cognitive conflict in the other conditions. However, even if studies on facilitation effects are extremely rare, some have indeed reported neural activity which was evoked by congruency, for instance, with the number-size congruity paradigm (Cohen Kadosh et al., 2008) or with Navon figures (Hedden & Gabrieli, 2010). Still, in the present study, during the response phase of the Numerical Stroop task no neural correlates were obtained, neither for facilitation nor for interference effects.

However, an alternative explanation is that the null findings result from a methodological issue, namely from the fast fMRI design which was used in the present study. Because functional MR imaging is based on the measurement of vascular changes, it has a very slow response time. Therefore, fast dynamics of neural processing, which proceed within milliseconds, are very difficult to capture. Its low temporal resolution is one of the main disadvantages of fMRI.

Especially in fast event-related fMRI designs, like the one used in the present study, the hemodynamic response function (HRF) is not allowed to return to baseline after stimulus presentation. In this case, the vascular changes which are evoked by the stimulus show an overlap with the changes evoked by the cue. Especially in those cases in which the changes occur at close temporal and spatial range and in which the hemodynamic response is not able to return to baseline activity, the BOLD changes are difficult to separate.

However, the time course of the BOLD signal is supposed to be very stable, and assumed to peak in a time window of four to six seconds. Hence according to Zarahn et al. (1997, p. 135) "the property of time-intensity separability should allow one to model (at least approximately) the fMRI changes associated with neural activity occurring during particular periods of time". In their report they also describe a trial-based design, which is very similar to the one used in the present study, namely "[f]unctional signal changes associated with different behavioral subcomponents within a trial were modeled separately" (Zarahn et al., 1997, p. 125). To do so, Zarahn et al. (1997) suggest to randomize the trials and, most importantly, to add variable inter-trial intervals (ITI) to be able to discriminate the functional changes in the BOLD signal. This is what was done in the present study (see Appendix, Table A.3). As suggested by Zarahn et al. (1997), the ITIs between stimulus and cue onset were short and amounted from 1.5 to 3 seconds.

However, there are some caveats. First, even if Zarahn et al. (1997) suggested to avoid a smoothing of the data, this was actually done in the present study, which may have resulted in the loss of data. Furthermore, for studies involving overt responses longer inter-stimulus intervals may be needed. According to Birn, Cox, and Bandettini (2004, p. 1046), for those studies "an event-related design with a minimum stimulus duration (SD) of 5 s and an average interstimulus interval (ISI) of 10 s were found to optimally detect blood oxygenation level-dependent signal changes without significant motion artifact". Hence, it might be argued that the signal was noisy due to motion artefacts during the response phase and that the data was mutilated.

However, what speaks against this argument is that the task network and the response network showed a large overlap for the Numerical Stroop task (see Appendix, Table A.4) and for the Picture-Word Interference task (see Appendix, Table A.5). The results indicate that the BOLD signals at the two time points were not completely indiscernible. Furthermore, in both paradigms neural correlates for the task as well as the response phase were detected.

Nevertheless, due to the temporal limitations of fMRI I believe that using a method with a higher temporal resolution such as MEG is an intriguing avenue for future research that might lead to detecting a dissociation between the neural mechanisms involved in retrieval and response conflicts, which would shed light on the distinct mechanisms for these stages.

7.5 Conclusion

In his review, MacLeod (1991) has mentioned the relationship between the (Colour-)Stroop task and the Picture-Word Interference task, stating "[T]he essential work of ascertaining empirically just how similar

the two tasks are remains to be performed. This is not a straightforward problem given the different sorts of questions being addressed in the two domains. One way to make some inroads would be through an individual-differences study examining the correlation between interference in the two tasks. The greater the comparability of results in the two tasks over the same individuals, the more confident we will be that they measure the same cognitive processes." (MacLeod, 1991, p. 168)

In this dissertation, this question was employed to the Numerical Stroop task and the Picture-Word Interference task:

The first hypothesis proposed was that the processing costs for both paradigms occur early in the processing stream, namely during the retrieval phase. Indeed, the results of my behavioural and fMRI experiments support this hypothesis. In both paradigms, reaction times were increased when the target and the distractor were presented simultaneously and the response was given immediately, but it was not present when the participants' response was delayed, indicating that interference had not occurred at the response stage. Moreover, in both paradigms, also the neural activation pattern of the interference effect during the retrieval phase is interpreted to reflect an increased cognitive demand. However, during the response phase, significant brain activation is not observed.

Hence, the neural activation pattern resembles the one obtained in the reaction times; both reflect competition during the selection of the target name.

The second hypothesis proposed was that the resolution of the conflict between target and distractor for number and object representations does not rely on common neural substrates. Indeed, a right posterior temporal region was sensitive to interference effects in the Numerical Stroop task, whereas the left middle temporal lobe was sensitive to interference in the Picture-Word Interference task. Because both do not share common neural substrates, it is concluded that cognitive conflicts in the number core system and in the object core system seem to be processed in distinct pathways.

Finally, given the question on the comparability of the results in the Numerical Stroop task and Picture-Word Interference task I conclude that they show a striking similarity in their temporal succession yet a vast difference in their underlying neuronal substrates.

References

Abdel Rahman, R., & Melinger, A. (2009). Semantic context effects in language production: A swinging lexical network proposal and a review. *Language and Cognitive Processes*, *24*(5), 713–734.

Abel, S., Dressel, K., Bitzer, R., Kümmerer, D., Mader, I., Weiller, C., & Huber, W. (2009). The separation of processing stages in a lexical interference fMRI-paradigm. *NeuroImage*, *44*(3), 1113–1124.

Abel, S., Dressel, K., Weiller, C., & Huber, W. (2012). Enhancement and suppression in a lexical interference fMRI-paradigm. *Brain and Behavior*, *2*(2), 109–127.

Abel, S., Huber, W., Weiller, C., Amunts, K., Eickhoff, S. B., & Heim, S. (2011). The influence of handedness on hemispheric interaction during word production: Insights from effective connectivity analysis. *Brain Connectivity*, *1*(3), 219–231.

Akirav, I., & Maroun, M. (2006). Ventromedial prefrontal cortex is obligatory for consolidation and reconsolidation of object recognition memory. *Cerebral Cortex*, *16*(12), 1759–1765.

Algom, D., Dekel, A., & Pansky, A. (1996). The perception of number from the separability of the stimulus: The Stroop effect revisited. *Memory & Cognition*, *24*(5), 557–572.

Amunts, K., Lenzen, M., Friederici, A. D., Schleicher, A., Morosan, P., Palomero-Gallagher, N., & Zilles, K. (2010). Broca's region: Novel organizational principles and multiple receptor mapping. *PLoS Biology*, *8*(9), e1000489.

Ansari, D., Fugelsang, J. A., Dhital, B., & Venkatraman, V. (2006). Dissociating response conflict from numerical magnitude processing in the brain: An event-related fMRI study. *NeuroImage*, *32*(2), 799–805.

Ansari, D., Lyons, I. M., van Eimeren, L., & Xu, F. (2007). Linking visual attention and number processing in the brain: The role of the temporo-parietal junction in small and large symbolic and nonsymbolic number comparison. *Journal of Cognitive Neuroscience*, *19*(11), 1845–1853.

Appelbaum, L., Meyerhoff, K., & Woldorff, M. (2009). Priming and backward influences in the human brain: Processing interactions during the Stroop interference effect. *Cerebral Cortex*, *19*(11), 2508–2521.

Aristei, S., & Abdel Rahman, R. (2013). Semantic interference in language production is due to graded similarity, not response relevance. *Acta Psychologica*, *144*(3), 571–582.

Aron, A. R., Durston, S., Eagle, D. M., Logan, G. D., Stinear, C. M., & Stuphorn, V. (2007). Converging evidence for a fronto-basal-ganglia network for inhibitory control of action and cognition. *The Journal of Neuroscience*, *27*(44), 11860–11864.

Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience*, *6*(2), 115–116.

Arsalidou, M., & Taylor, M. J. (2011). Is $2 + 2 = 4$? Meta-analyses of brain areas needed for numbers and calculations. *NeuroImage*, *54*(3), 2382–2393.

Attout, L., Fias, W., Salmon, E., & Majerus, S. (2014). Common neural substrates for ordinal representation in short-term memory, numerical and alphabetical cognition. *PLoS ONE*, *9*(3), e92049.

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*(10), 829–839.

Badre, D., Lebrecht, S., Pagliaccio, D., Long, N. M., & Scimeca, J. M. (2014). Ventral striatum and the evaluation of memory retrieval strategies. *Journal of Cognitive Neuroscience*, *26*(9), 1928–1948.

Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, *47*(6), 907–918.

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., ... others (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(2), 449–454.

Bar, M., Tootell, R. B., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., ... Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron*, *29*(2), 529–535.

Barber, A. D., Caffo, B. S., Pekar, J. J., & Mostofsky, S. H. (2013). Effects of working memory demand on neural mechanisms of motor response selection and control. *Journal of Cognitive Neuroscience*, *25*(8), 1235–1248.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi: 10.18637/jss.v067.i01

Bear, M. F., Connors, B. W., & Paradiso, M. A. (2007). *Neuroscience* (Vol. 2). Lippincott Williams & Wilkins.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–2796.

Birn, R. M., Cox, R. W., & Bandettini, P. A. (2004). Experimental designs and processing strategies for fMRI studies involving overt verbal responses. *NeuroImage*, *23*(3), 1046–1058.

Bledowski, C., Rahm, B., & Rowe, J. B. (2009). What "works" in working memory? Separate systems for selection and updating of critical information. *The Journal of Neuroscience*, *29*(43), 13735–13741.

Boersma, P., & Weenink, D. (2012, October). *Praat: Doing phonetics by computer.* http://www.praat.org/. (computer program)

Bohle, H. S. (2010). *Wettbewerb in der Sprachproduktion: Ist semantische Interferenz ein lexikalisches oder postlexikalisches Phänomen?* (unpublished master thesis)

Bonner, M. F., & Price, A. R. (2013). Where is the anterior temporal lobe and what does it do? *The Journal of Neuroscience*, *33*(10), 4213–4215.

Botvinick, M. M. (2007). Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(4), 356–366.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624.

brainmap.org. (2015, July). *GingerALE 2.3.3.* http://www.brainmap.org. (computer program)

Brass, M., Derrfuss, J., Forstmann, B., & von Cramon, D. Y. (2005). The role of the inferior frontal junction area in cognitive control. *Trends in Cognitive Sciences*, *30*, 45–57.

Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: Emerging methods and principles. *Trends in Cognitive Sciences*, *14*(6), 277–290.

Bulthé, J., De Smedt, B., & Op De Beeck, H. (2014). Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. *NeuroImage*, *87*, 311–322.

Bush, G., Frazier, J. A., Rauch, S. L., Seidman, L. J., Whalen, P. J., Jenike, M. A., ... Biederman, J. (1999). Anterior cingulate cortex dysfunction in attention-deficit/hyperactivity disorder revealed by fMRI and the counting Stroop. *Biological Psychiatry*, *45*(12), 1542–1552.

Bush, G., Whalen, P., Rosen, B., Jenike, M., McInerney, S., & Rauch, S. (1998). The counting Stroop: An interference task specialized for functional neuroimaging – validation study with functional MRI. *Human Brain Mapping*, *6*, 270–282.

Bush, G., Whalen, P. J., Shin, L. M., & Rauch, S. L. (2006). The Counting Stroop: A cognitive interference task. *Nature Protocols*, *1*(1), 230.

Cappelletti, M., Butterworth, B., & Kopelman, M. (2001). Spared numerical abilities in a case of semantic dementia. *Neuropsychologia*, *39*(11), 1224–1239.

Caramazza, A. (1997). How many levels of processing are there in lexical access? *Cognitive Neuropsychology*, *14*(1), 177–208.

Cattell, J. M. (1886). The time it takes to see and name objects. *Mind*, *11*(41), 63–65.

Chang, C.-F., Hsu, T.-Y., Tseng, P., Liang, W.-K., Tzeng, O. J., Hung, D. L., & Juan, C.-H. (2013). Right temporoparietal junction and attentional reorienting. *Human Brain Mapping*, *34*(4), 869–877.

Chassy, P., & Grodd, W. (2012). Comparison of quantities: Core and format-dependent regions as revealed by fMRI. *Cerebral Cortex*, *22*(6), 1420–1430.

Chen, Z., Lei, X., Ding, C., Li, H., & Chen, A. (2013). The neural mechanisms of semantic and response conflicts: An fMRI study of practice-related effects in the Stroop task. *NeuroImage*, *66*(4), 577–584.

Chesney, D. L., & Haladjian, H. H. (2011). Evidence for a shared mechanism used in multiple-object tracking and subitizing. *Attention, Perception, & Psychophysics*, *73*(8), 2457–2480.

Chochon, F., Cohen, L., Van De Moortele, P., & Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. *Journal of Cognitive Neuroscience*, *11*(6), 617–630.

Cieslik, E. C., Mueller, V. I., Eickhoff, C. R., Langner, R., & Eickhoff, S. B. (2015). Three key regions for supervisory attentional control: Evidence from neuroimaging meta-analyses. *Neuroscience & Biobehavioral Reviews*, *48*, 22–34.

Cieslik, E. C., Zilles, K., Caspers, S., Roski, C., Kellermann, T. S., Jakobs, O., ... Eickhoff, S. B. (2012). Is there "one" DLPFC in cognitive action control? Evidence for heterogeneity from co-activation-based parcellation. *Cerebral Cortex*, 2677-2689.

Clarke, A., Taylor, K. I., Devereux, B., Randall, B., & Tyler, L. K. (2012). From perception to conception: How meaningful objects are processed over time. *Cerebral Cortex*, *23*(1), 1–9.

Coderre, E., Conklin, K., & van Heuven, W. J. (2011). Electrophysiological measures of conflict detection and resolution in the Stroop task. *Brain Research*, *1413*, 51–59.

Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain*, *125*(5), 1054–1069.

Cohen Kadosh, R., Cohen Kadosh, K., Henik, A., & Linden, D. E. (2008). Processing conflicting information: Facilitation, interference, and functional connectivity. *Neuropsychologia*, *46*(12), 2872–2879.

Cohen Kadosh, R., Gevers, W., & Notebaert, W. (2011). Sequential analysis of the Numerical Stroop effect reveals response suppression. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*(5), 1243.

Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., van de Ven, V., ... Linden, D. E. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, *43*(9), 1238–1248.

Cohen Kadosh, R., & Walsh, V. (2009). Numerical representation in the parietal lobes: Abstract or not abstract? *Behavioral and Brain Sciences*, *32*(3-4), 313–328.

Condry, K. F., & Spelke, E. S. (2008). The development of language and abstract concepts: The case of natural number. *Journal of Experimental Psychology: General*, *137*(1), 22.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215.

Coubart, A., Izard, V., Spelke, E. S., Marie, J., & Streri, A. (2014). Dissociation between small and large numerosities in newborn infants. *Developmental Science*, *17*(1), 11–22.

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*, *6*(1), 39–49.

Crosson, B., Benefield, H., Cato, M. A., Sadek, J. R., Moore, A. B., Wierenga, C. E., ... Auerbach, E. J. (2003). Left and right basal ganglia and frontal activity during language generation: Contributions to lexical, semantic, and phonological processes. *Journal of the International Neuropsychological Society*, *9*(07), 1061–1077.

Cusack, R., Mitchell, D. J., & Duncan, J. (2009). Discrete object representation, attention switching, and task difficulty in the parietal lobe. *Journal of Cognitive Neuroscience*, *22*(1), 32–47.

Cutini, S., Scarpa, F., Scatturin, P., Dell'Acqua, R., & Zorzi, M. (2012). Number–space interactions in the human parietal cortex: Enlightening the SNARC effect with functional near-infrared spectroscopy. *Cerebral Cortex*, 1–8.

Cutini, S., Scatturin, P., Basso Moro, S., & Zorzi, M. (2014). Are the neural correlates of subitizing and estimation dissociable? A fNIRS investigation. *NeuroImage*, *85*, 391–399.

Dale, A. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping*, *8*(2-3), 109–114.

Damian, M. F., & Bowers, J. S. (2003). Locus of semantic interference in Picture-Word Interference tasks. *Psychonomic Bulletin and Review*, *10*(1), 111–117.

De Beeck, H. P. O., Torfs, K., & Wagemans, J. (2008). Perceived shape similarity among unfamiliar objects and the organization of the human object vision pathway. *The Journal of Neuroscience*, *28*(40), 10111–10123.

Dehaene, S. (1996). The organization of brain activations in number comparison: Event-related potentials and the additive-factors method. *Journal of Cognitive Neuroscience*, *8*(1), 47–68.

Dehaene, S. (2011). *The Number Sense: How the Mind Creates Mathematics*. New York NY: Oxford University Press. (First published in 1997; Revised & Expanded Edition)

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology General*, *122*, 371–371.

Dehaene, S., & Cohen, L. (1996). Towards an anatomical and functional model of number processing. *Mathematical Cognition*, *1*, 83–120.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex*, *33*(2), 219–250.

Dehaene, S., Molko, N., Cohen, L., & Wilson, A. J. (2004). Arithmetic and the brain. *Current Opinion in Neurobiology*, *14*(2), 218–224.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3), 487–506.

Dehaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological Science*, *5*(5), 303–305.

De Houwer, J. (2003). On the role of stimulus-response and stimulus-stimulus compatibility in the Stroop effect. *Memory & Cognition*, *31*(3), 353–359.

Deichmann, R. (2005). Fast high-resolution T1 mapping of the human brain. *Magnetic Resonance in Medicine*, *54*(1), 20–27.

Dell, G. S. (1986). A spreading-activation theory of retrieval in sentence production. *Psychological Review*, *93*(3), 283.

Dell, G. S., & O'Seaghdha, P. G. (1992). Stages of lexical access in language production. *Cognition*, *42*(1), 287–314.

Dell, G. S., Schwartz, M., Martin, N., Saffran, E., & Gagnon, D. (1997). Lexical access in aphasic and nonaphasic speakers. *Psychological Review*, *104*(4), 801–838.

Dell'Acqua, R., Job, R., Peressotti, F., & Pascali, A. (2007). The Picture-Word Interference effect is not a Stroop effect. *Psychonomic Bulletin and Review*, *14*(4), 717–722.

Dell'Acqua, R., Pesciarelli, F., Jolicœur, P., Eimer, M., & Peressotti, F. (2007). The interdependence of spatial attention and lexical access as revealed by early asymmetries in occipito-parietal ERP activity. *Psychophysiology*, *44*(3), 436–443.

Dell'Acqua, R., Sessa, P., Peressotti, F., Mulatti, C., Navarrete, E., & Grainger, J. (2010). ERP evidence for ultra-fast semantic processing in the Picture-Word Interference paradigm. *Frontiers in Psychology*, *1*, 177.

Derrfuss, J., Brass, M., Neumann, J., & von Cramon, D. Y. (2005). Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and Stroop studies. *Human Brain Mapping*, *25*(1), 22–34.

Derrfuss, J., Brass, M., & von Cramon, D. Y. (2004). Cognitive control in the posterior frontolateral cortex: Evidence from common activations in task coordination, interference control, and working memory. *NeuroImage*, *23*(2), 604.

De Zubicaray, G. I., Hansen, S., & McMahon, K. L. (2013). Differential processing of thematic and categorical conceptual relations in spoken word production. *Journal of Experimental Psychology: General*, *142*(1), 131–141.

De Zubicaray, G. I., Johnson, K., Howard, D., & McMahon, K. (2014). A perfusion fMRI investigation of thematic and categorical context effects in the spoken production of object names. *Cortex*, *54*, 135–149.

De Zubicaray, G. I., Wilson, S. J., McMahon, K. L., & Muthiah, S. (2001). The semantic interference effect in the picture-word paradigm: An event-related fMRI study employing overt responses. *Human Brain Mapping*, *14*(4), 218–227.

Dhooge, E., & Hartsuiker, R. J. (2010). The distractor frequency effect in Picture-Word Interference: Evidence for Response Exclusion. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*(4), 878.

Dhooge, E., & Hartsuiker, R. J. (2011). The distractor frequency effect in a delayed Picture-Word Interference task: Further evidence for a late locus of distractor exclusion. *Psychonomic Bulletin and Review*, *18*(1), 116–122.

Diaz, M. T., Hogstrom, L. J., Zhuang, J., Voyvodic, J. T., Johnson, M. A., & Camblin, C. C. (2014). Written distractor words influence brain activity during overt picture naming. *Frontiers in Human Neuroscience*, *24*(8), 164–170.

DiCarlo, J. J., & Cox, D. D. (2007). Untangling invariant object recognition. *Trends in Cognitive Sciences*, *11*(8), 333–341.

DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron*, *73*(3), 415–434.

Di Russo, F., Martínez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping*, *15*(2), 95–111.

Dyer, F. N. (1971). The duration of word meaning responses: Stroop interference for different preexposures of the word. *Psychonomic Science*, *25*(4), 229–231.

Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering cortical number coding from human brain activity patterns. *Current Biology*, *19*(19), 1608–1615.

Eger, E., Sterzer, P., Russ, M. O., Giraud, A.-L., & Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, *37*(4), 719–726.

Eickhoff, S. B., Paus, T., Caspers, S., Grosbras, M.-H., Evans, A. C., Zilles, K., & Amunts, K. (2007). Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. *NeuroImage*,

36(3), 511–521.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, *25*(4), 1325–1335.

Erez, J., Cusack, R., Kendall, W., & Barense, M. D. (2015). Conjunctive coding of complex object features. *Cerebral Cortex*, 1–12.

Ester, E. F., Drew, T., Klee, D., Vogel, E. K., & Awh, E. (2012). Neural measures reveal a fixed item limit in subitizing. *The Journal of Neuroscience*, *32*(21), 7169–7177.

Fagot, C., & Pashler, H. (1992). Making two responses to a single object: Implications for the central attentional bottleneck. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(4), 1058.

Fan, L.-Y., Gau, S.-F., & Chou, T.-L. (2014). Neural correlates of inhibitory control and visual processing in youths with attention deficit hyperactivity disorder: A counting Stroop functional MRI study. *Psychological Medicine*, *44*(12), 2661–2671.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307–314.

Ferreira, C. T., Ceccaldi, M., Giusiano, B., & Poncet, M. (1998). Separate visual pathways for perception of actions and objects: Evidence from a case of apperceptive agnosia. *Journal of Neurology, Neurosurgery & Psychiatry*, *65*(3), 382–385.

Fias, W., Lammertyn, J., Caessens, B., & Orban, G. A. (2007). Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. *The Journal of Neuroscience*, *27*(33), 8952–8956.

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., & Orban, G. A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience*, *15*(1), 47–56.

Fias, W., Reynvoet, B., & Brysbaert, M. (2001). Are Arabic numerals processed as pictures in a Stroop interference task? *Psychological Research*, *65*(4), 242–249.

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature*, *382*(6592), 626 - 628.

Finkbeiner, M., & Caramazza, A. (2006). Now you see it, now you don't: On turning semantic interference into facilitation in a Stroop-like task. *Cortex*, *42*(6), 790–796.

Forster, K., & Forster, J. (2003). DMDX: A Windows display program with millisecond accuracy. *Behavior Research Methods Instruments and Computers*, *35*(1), 116–124.

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences*, *16*(5), 262–268.

Friederici, A. D., & Gierhan, S. M. (2013). The language network. *Current Opinion in Neurobiology*, *23*(2), 250–254.

Friedrich, R. M., & Friederici, A. D. (2009). Mathematical logic in the human brain: Syntax. *PLoS ONE*, *4*(5), e5599.

Friedrich, R. M., & Friederici, A. D. (2013). Mathematical logic in the human brain: Semantics. *PLoS ONE*, *8*(1), e53699.

Fulbright, R. K., Manson, S. C., Skudlarski, P., Lacadie, C. M., & Gore, J. C. (2003). Quantity determination and the distance effect with letters, numbers, and shapes: A functional MR imaging study of number processing. *American Journal of Neuroradiology*, *24*(2), 193–200.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition*, *44*(1), 43–74.

Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, *4*(2), 59–65.

Gasquoine, P. G. (2013). Localization of function in anterior cingulate cortex: From psychosurgery to functional neuroimaging. *Neuroscience & Biobehavioral Reviews*, *37*(3), 340 - 348.

Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2002). *Cognitive Neurosciences: The Biology of Mind* (2nd ed.). New York: Cambridge University Press.

Gläscher, J. (2009). Visualization of group inference data in functional neuroimaging. *Neuroinformatics*, *7*(1), 73–82.

Gläscher, J., & Gitelman, D. (2008). Contrast weights in flexible factorial design with multiple groups of subjects. *SPM@ JISCMAIL. AC. UK) Sml, editor*.

Glaser, M. O., & Glaser, W. R. (1982). Time course analysis of the Stroop phenomenon. *Journal of Experimental Psychology: Human Perception and Performance*, *8*(6), 875–880.

Glaser, W., & Düngelhoff, F. (1984). The time course of Picture-Word Interference. *Journal of Experimental Psychology: Human Perception and Performance*, *10*(5), 640–654.

Goldrick, M., Dell, G., Kroll, J., & Rapp, B. (2009). Sequential information processing and limited interaction in language production. *Online Letters to Science*, *13*(1).

Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within broca's area. *NeuroImage*, *114*(1), 294-302.

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision research*, *41*(10), 1409–1422.

Gur, R. C., Turetsky, B. I., Loughead, J., Waxman, J., Snyder, W., Ragland, J. D., ... Gur, R. E. (2007). Hemodynamic responses in neural circuitries for detection of visual target and novelty: An event-related fMRI study. *Human brain mapping*, *28*(4), 263–274.

Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: Inhibition and attentional control. *NeuroImage*, *50*(3), 1313–1319.

Hanslmayr, S., Pastötter, B., Bäuml, K.-H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the Stroop task. *Journal of Cognitive Neuroscience*, *20*(2), 215–225.

Hedden, T., & Gabrieli, J. D. (2010). Shared and selective neural correlates of inhibition, facilitation, and shifting processes during executive control. *NeuroImage*, *51*(1), 421–431.

Hickok, G. (2014). The architecture of speech production and the role of the phoneme in speech processing. *Language, Cognition and Neuroscience*, *29*(1), 2–20.

Holloway, I. D., Price, G. R., & Ansari, D. (2010). Common and segregated neural pathways for the processing of symbolic and nonsymbolic numerical magnitude: An fMRI study. *NeuroImage*, *49*(1), 1006–1017.

Hyde, D. C., & Spelke, E. S. (2011). Neural signatures of number processing in human infants: evidence for two core systems underlying numerical cognition. *Developmental science*, *14*(2), 360–371.

Indefrey, P. (2011). The spatial and temporal signatures of word production components: A critical update. *Frontiers in Psychology*, *2*.

Indefrey, P., & Levelt, W. (2004). The spatial and temporal signatures of word production components. *Cognition*, *92*(1-2), 101–44.

Ischebeck, A. (2003). Differences between digit naming and number word reading in a flanker task. *Memory & Cognition*, *31*(4), 529–537.

Izard, V., Sann, C., Spelke, E., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences*, *106*(25), 10382–10385.

Jakobs, O., Langner, R., Caspers, S., Roski, C., Cieslik, E. C., Zilles, K., ... Eickhoff, S. B. (2012). Across-study and within-subject functional connectivity of a right temporo-parietal junction subregion involved in stimulus–context integration. *NeuroImage*, *60*(4), 2389–2398.

Jankowiak, J., Kinsbourne, M., Shalev, R. S., & Bachman, D. L. (1992). Preserved visual imagery and categorization in a case of associative visual agnosia. *Journal of Cognitive Neuroscience*, *4*(2), 119–131.

Janssen, N., Schirm, W., Mahon, B., & Caramazza, A. (2008). Semantic interference in a delayed naming task: Evidence for the Response Exclusion hypothesis. *Learning, Memory and Cognition*, *34*(1), 249–256.

Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: A case-series comparison. *Brain*, *129*(8), 2132–2147.

Kaufmann, L., Koppelstaetter, F., Delazer, M., Siedentopf, C., Rhomberg, P., Golaszewski, S., ... Ischebeck, A. (2005). Neural correlates of distance and congruity effects in a Numerical Stroop task: An event-related fMRI study. *NeuroImage*, *25*(3), 888-898.

Kaufmann, L., Wood, G., Rubinsten, O., & Henik, A. (2011). Meta-analyses of developmental fMRI studies investigating typical and atypical trajectories of number processing and calculation. *Developmental Neuropsychology*, *36*(6), 763–787.

Kim, C., Chung, C., & Kim, J. (2010). Multiple cognitive control mechanisms associated with the nature of conflict. *Neuroscience Letters*, *476*(3), 156–160.

Kim, C., Cilles, S. E., Johnson, N. F., & Gold, B. T. (2012). Domain general and domain preferential brain regions associated with different types of task switching: A meta-analysis. *Human Brain Mapping*, *33*(1), 130–142.

Kim, C., Johnson, N. F., Cilles, S. E., & Gold, B. T. (2011). Common and distinct mechanisms of cognitive flexibility in prefrontal cortex. *The Journal of neuroscience*, *31*(13), 4771–4779.

Klein, E., Suchan, J., Moeller, K., Karnath, H.-O., Knops, A., Wood, G., ... Willmes, K. (2014). Considering structural connectivity in the triple code model of numerical cognition: Differential connectivity for magnitude processing and arithmetic facts. *Brain Structure and Function*, *221*(2), 979-295.

Klein, G. (1964). Semantic power measured through the interference of words with color-naming. *The American Journal of Psychology*, *77*(1), 576–588.

Koechlin, E., Naccache, L., Block, E., & Dehaene, S. (1999). Primed numbers: exploring the modularity of numerical representations with masked and unmasked semantic priming. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(6), 1882.

Koelsch, S., Schulze, K., Sammler, D., Fritz, T., Müller, K., & Gruber, O. (2009). Functional architecture of verbal and tonal working memory: An fMRI study. *Human Brain Mapping*, *30*(3), 859–873.

Kotz, S. A., Cappa, S. F., von Cramon, D. Y., & Friederici, A. D. (2002). Modulation of the lexical–semantic network by auditory semantic priming: An event-related functional MRI study. *NeuroImage*, *17*(4), 1761–1772.

Krall, S., Rottschy, C., Oberwelland, E., Bzdok, D., Fox, P., Eickhoff, S., ... Konrad, K. (2014). The role of the right temporoparietal junction in attention and social interaction as revealed by ALE meta-analysis. *Brain Structure and Function*, *220*(2), 587–604.

Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., ... Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, *10*(3), 120–131.

Levelt, W. (1989). *Speaking: From Intention to Articulation*. Cambridge: MA.

Levelt, W. (1992). Accessing words in speech production: Stages, processes and representations. In W. Levelt (Ed.), *Lexical access in speech production* (pp. 1–22). Amsterdam: Blackwell.

Levelt, W. (1999). Models of word production. *Trends in Cognitive Sciences*, *3*(6), 223–232.

Levelt, W., Roelofs, A., & Meyer, A. (1999). A theory of lexical access in speech production. *Behavioral and Brain Sciences*, *22*(1), 1–75.

Levelt, W., Schriefers, H., Vorberg, D., Meyer, A., Pechmann, T., & Havinga, J. (1991). The time course of lexical access in speech production: A study of picture naming. *Psychological Review*, *98*(1), 122–142.

Levy, B. J., & Wagner, A. D. (2011). Cognitive control and right ventrolateral prefrontal cortex: Reflexive reorienting, motor inhibition, and action updating. *Annals of the New York Academy of Sciences*, *1224*(1), 40–62.

Lindemann, O., Rueschemeyer, S.-A., & Bekkering, H. (2009). Symbols in numbers: From numerals to magnitude information. *Behavioral and Brain Sciences*, *32*(3-4), 341–342.

Liu, X., Wang, H., Corbly, C. R., Zhang, J., & Joseph, J. E. (2006). The involvement of the inferior parietal cortex in the Numerical Stroop effect and the distance effect in a two-digit number comparison task. *Journal of Cognitive Neuroscience*, *18*(9), 1518–1530.

Luo, C. R. (1999). Semantic competition as the basis of Stroop interference: Evidence from color-word matching tasks. *Psychological Science*, *10*(1), 35–40.

MacLaren, D. (2014). *Google Forum on 'Aaron's fMRI matlab tools' (GLM-FLEX)*. Retrieved from `http://bit.ly/1M4zU8J`

MacLaren, D. (2015). *Jiscmail forum on Statistical Parametric Mapping (SPM)*. Retrieved from `http://bit.ly/1LOf22f`

MacLeod, C. (1991). Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin*, *109*, 162–203.

MacLeod, C., & MacDonald, P. (2000). Interdimensional interference in the Stroop effect: Uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences*, *4*(10), 383–391.

Mädebach, A., Oppermann, F., Hantsch, A., Curda, C., & Jescheniak, J. D. (2011). Is there semantic interference in delayed naming? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*(2), 522–538.

Maess, B., Friederici, A. D., Damian, M., Meyer, A. S., & Levelt, W. J. (2002). Semantic category interference in overt picture naming: Sharpening current density localization by PCA. *Journal of Cognitive Neuroscience*, *14*(3), 455–462.

Mahon, B. Z., Costa, A., Peterson, R., Vargas, K. A., & Caramazza, A. (2007). Lexical selection is not by competition: A reinterpretation of semantic interference and facilitation effects in the Picture-Word Interference paradigm. *Journal of Experimental Psychology*, *33*(3), 503–535.

Makuuchi, M., Bahlmann, J., Anwander, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of*

Sciences, *106*(20), 8362–8367.

Makuuchi, M., & Friederici, A. D. (2013). Hierarchical functional connectivity between the core language system and the working memory system. *Cortex*, *49*(9), 2416–2423.

Malach, R., Reppas, J., Benson, R., Kwong, K., Jiang, H., Kennedy, W., ... Tootell, R. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences*, *92*(18), 8135–8139.

Matsumoto, K., & Tanaka, K. (2004). Conflict and cognitive control. *Science*, *303*(5660), 969–970.

McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, Panthera leo. *Animal Behaviour*, *47*(2), 379–387.

Mehler, J., & Bever, T. G. (1967). Cognitive capacity of very young children. *Science*, *158*(3797), 171–172.

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure and Function*, *214*(5-6), 655–667.

Meyer, A. S., & Damian, M. F. (2007). Activation of distractor names in the Picture-Picture Interference paradigm. *Memory & cognition*, *35*(3), 494–503.

Miezin, F. M., Maccotta, L., Ollinger, J., Petersen, S., & Buckner, R. (2000). Characterizing the hemodynamic response: Effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. *NeuroImage*, *11*(6), 735–759.

Mirman, D., & Graziano, K. M. (2012). Damage to temporo-parietal cortex decreases incidental activation of thematic relations during spoken word comprehension. *Neuropsychologia*, *50*(8), 1990–1997.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.

Morsella, E., & Miozzo, M. (2002). Evidence for a cascade model of lexical access in speech production. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 555.

Moyer, R., & Landauer, T. (1967). Time required for judgements of numerical inequality. *Nature*, *215*, 1519–1520.

Muehlhaus, J., Heim, S., Altenbach, F., Chatterjee, A., Habel, U., & Sass, K. (2014). Deeper insights into semantic relations: An fMRI study of part-whole and functional associations. *Brain and Language*, *129*, 30–42.

Nee, D. E., Brown, J. W., Askren, M. K., Berman, M. G., Demiralp, E., Krawitz, A., & Jonides, J. (2013). A meta-analysis of executive components of working memory. *Cerebral Cortex*, *23*(2), 264–282.

Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(1), 1–17.

Neubert, F.-X., Mars, R. B., & Rushworth, M. (2013). Is there an inferior frontal cortical network for cognitive control and inhibition. *Principles of frontal lobe function, Ed*, *2*, 332–352.

Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J.-B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage*, *25*(3), 653–660.

Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science*, *297*(5587), 1708–1711.

Noonan, K. A., Jefferies, E., Corbett, F., & Lambon Ralph, M. A. (2010). Elucidating the nature of deregulated semantic cognition in semantic aphasia: Evidence for the roles of prefrontal and temporo-parietal cortices. *Journal of Cognitive Neuroscience*, *22*(7), 1597–1613.

Pagano, S., & Mazza, V. (2013). Multiple object individuation during Numerical Stroop. *Psychophysiology*, *25*(5), 697–705.

Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological bulletin*, *116*(2), 220–222.

Paucke, M., Oppermann, F., Koch, I., & Jescheniak, J. D. (2015). On the costs of parallel processing in dual-task performance: The case of lexical processing in word production. *Journal of Experimental Psychology: Human Perception and Performance*, 1–14.

Peelen, M. V., & Caramazza, A. (2012). Conceptual object representations in human anterior temporal cortex. *The Journal of Neuroscience*, *32*(45), 15728–15736.

Pessoa, L., & Ungerleider, L. G. (2004). Neural correlates of change detection and change blindness in a working memory task. *Cerebral Cortex*, *14*(5), 511–520.

Piai, V., Roelofs, A., Acheson, D. J., & Takashima, A. (2013). Attention for speaking: Domain-general control from the anterior cingulate cortex in spoken word production. *Frontiers in Human Neuroscience*, *7*.

Piai, V., Roelofs, A., & Schriefers, H. (2011). Semantic interference in immediate and delayed naming and reading: Attention and task decisions. *Journal of Memory and Language*, *64*(4), 404–423.

Piai, V., Roelofs, A., & Schriefers, H. (2014). Locus of semantic interference in picture naming: Evidence from dual-task performance. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*(1), 147.

Piai, V., Roelofs, A., & van der Meij, R. (2012). Event-related potentials and oscillatory brain responses associated with semantic and stroop-like interference effects in overt naming. *Brain Research*, *1450*, 87–101.

Piazza, M., & Dehaene, S. (2008). From Number Neurons to Mental Arithmetic: The Cognitive Neuroscience of Number Sense. In M. Gazzaniga (Ed.), *The Cognitive Neuroscience* (3rd ed., pp. 865–876). Cambridge: The MIT Press.

Piazza, M., Fumarola, A., Chinello, A., & Melcher, D. (2011). Subitizing reflects visuo-spatial object individuation capacity. *Cognition*, *121*(1), 147–153.

Piazza, M., & Izard, V. (2009). How humans count: Numerosity and the parietal cortex. *The Neuroscientist*, *15*(3), 261–273.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*(3), 547–555.

Piazza, M., Mechelli, A., Butterworth, B., & Price, C. (2002). Are subitizing and counting implemented as separate or functionally overlapping processes? *NeuroImage*, *15*(2), 435–446.

Piazza, M., Mechelli, A., Price, C. J., & Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: An fMRI study. *Brain Research*, *1106*(1), 177–188.

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron*, *53*(2), 293–305.

Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and approximate arithmetic in an Amazonian indigene group. *Science*, *306*(5695), 499–503.

Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage*, *14*(5), 1013–1026.

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, *41*(6), 983–993.

Pochon, J.-B., Riis, J., Sanfey, A. G., Nystrom, L. E., & Cohen, J. D. (2008). Functional imaging of decision conflict. *The Journal of Neuroscience*, *28*(13), 3468–3473.

Price, C. J. (2010). The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, *1191*(1), 62–88.

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage*, *62*(2), 816–847.

Protopapas, A. (2007). CheckVocal: A program to facilitate checking the accuracy and response time of vocal responses from DMDX. *Behavior Research Methods*, *39*(4), 859.

Quasthoff, U., Richter, M., & Biemann, C. (2006). Corpus portal for search in monolingual corpora. In *Proceedings of the fifth international conference on language resources and evaluation, lrec 2006*. Genoa: European Language Resources Association.

R Core Team. (2014). R: a language and environment for statistical computing [Computer software manual]. Vienna, Austria. Retrieved from `http://www.R-project.org`

Ratinckx, E., & Brysbaert, M. (2002). Interhemispheric stroop-like interference in number comparison: Evidence for strong interhemispheric integration of semantic number information. *Neuropsychology*, *16*(2), 217.

Regolin, L., & Vallortigara, G. (1995). Perception of partly occluded objects by young chicks. *Perception & Psychophysics*, *57*(7), 971–976.

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect numerical estimation? *Psychological Science*, *19*(6), 607–614.

Riesenhuber, M., & Poggio, T. (2000). Models of object recognition. *Nature Neuroscience*, *3*, 1199–1204.

Riesenhuber, M., & Poggio, T. (2002). Neural mechanisms of object recognition. *Current Opinion in Neurobiology*, *12*(2), 162–168.

Roelofs, A. (1992). A spreading activation theory of lemma retrieval in speaking. *Cognition*, *42*(1), 107–142.

Roelofs, A. (1997). The WEAVER model of word-form encoding in speech production. *Cognition*, *64*(3), 249–284.

Roelofs, A. (2002). Modeling of lexical access in speech production: A psycholinguistic perspective on the lexicon. In L. Behrens & D. Zaefferer (Eds.), *The Lexicon in Focus: Competition and Convergence*

in Current Lexicology (p. 75-92). Frankfurt am Main: Lang.

Roelofs, A. (2003). Goal-referenced selection of verbal action: Modeling attentional control in the Stroop task. *Psychological Review*, *110*(1), 88.

Roelofs, A., & Piai, V. (2013). Associative facilitation in the Stroop task: Comment on Mahon et al. (2012). *Cortex*, *49*(6), 1767–1769.

Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural neurology*, *12*(4), 191–200.

Rossion, B., & Pourtois, G. (2004). Revisiting snodgrass and vanderwart's object set: The role of surface detail in basic-level object recognition. *Perception*, *13*, 217-236. Letzter Abruf Juli 2009, von `http://titan.cog.brown.edu:8080/TarrLab/stimuli/objects/svlo.zip/view`.

Santens, S., & Gevers, W. (2008). The SNARC effect does not imply a mental number line. *Cognition*, *108*(1), 263–270.

Schendan, H. E., & Lucia, L. C. (2010). Object-sensitive activity reflects earlier perceptual and later cognitive processing of visual objects between 95 and 500ms. *Brain Research*, *1329*, 124–141.

Schmidt, J. R., & Cheesman, J. (2005). Dissociating stimulus-stimulus and response-response effects in the Stroop task. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, *59*(2), 132.

Schnur, T. T., & Martin, R. (2012). Semantic Picture-Word Interference is a postperceptual effect. *Psychonomic Bulletin and Review*, *19*(2), 301–308.

Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: Convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proceedings of the National Academy of Sciences*, *106*(1), 322–327.

Schriefers, H., Meyer, A. S., & Levelt, W. J. (1990). Exploring the time course of lexical access in language production: Picture-Word Interference studies. *Journal of Memory and Language*, *29*(1), 86–102.

Schuhmann, T., Schiller, N. O., Goebel, R., & Sack, A. T. (2011). Speaking of which: Dissecting the neurocognitive network of language production in picture naming. *Cerebral Cortex*, *22*(3), 701–709.

Schultz, A., & McLaren, D. (2014). *Glm flex.* `http://mrtools.mgh.harvard.edu/index.php/Main_Page`.

Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. *The Journal of Neuroscience*, *30*(50), 16809–16817.

Seymour, P. H. (1977). Conceptual encoding and locus of the Stroop effect. *The Quarterly Journal of Experimental Psychology*, *29*(2), 245–265.

Shenhav, A., Straccia, M. A., Cohen, J. D., & Botvinick, M. M. (2014). Anterior cingulate engagement in a foraging context reflects choice difficulty, not foraging value. *Nature Neuroscience*, *17*(9), 1249–1254.

Siegler, R. S., & Opfer, J. E. (2003). The development of numerical estimation evidence for multiple representations of numerical quantity. *Psychological Science*, *14*(3), 237–250.

Silver, M. A., Ress, D., & Heeger, D. J. (2007). Neural correlates of sustained spatial attention in human early visual cortex. *Journal of Neurophysiology*, *97*(1), 229–237.

Sneve, M. H., Magnussen, S., Alnæs, D., Endestad, T., & D'Esposito, M. (2013). Top–down modulation from inferior frontal junction to fefs and intraparietal sulcus during short-term memory for visual features. *Journal of Cognitive Neuroscience*, *25*(11), 1944–1956.

Soltész, F., Szűcs, D., Dékány, J., Márkus, A., & Csépe, V. (2007). A combined event-related potential and neuropsychological investigation of developmental dyscalculia. *Neuroscience Letters*, *417*(2), 181–186.

Song, X.-W., Dong, Z.-Y., Long, X.-Y., Li, S.-F., Zuo, X.-N., Zhu, C.-Z., ... Zang, Y.-F. (2011). Rest: A toolkit for resting-state functional magnetic resonance imaging data processing. *PLoS ONE*, *6*(9), e25031.

Spelke, E. (2000). Core knowledge. *American Psychologist*, *55*(1), 1233–1243.

Spelke, E. (2003). What makes us smart? Core knowledge and natural language. *Language in mind: Advances in the study of language and thought*, 277–311.

Spelke, E., & Kinzler, K. D. (2007). Core knowledge. *Developmental Science*, *10*(1), 89–96.

Spelke, E., & Tsivkin, S. (2001). Language and number: A bilingual training study. *Cognition*, *78*(1), 45–88.

Statistical parametric mapping. (2009, April). http://www.fil.ion.ucl.ac.uk/spm/software/spm8/. (computer program)

Strobel, A., Debener, S., Sorger, B., Peters, J. C., Kranczioch, C., Hoechstetter, K., ... Goebel, R. (2008). Novelty and target processing during an auditory novelty oddball: a simultaneous event-related potential and functional magnetic resonance imaging study. *NeuroImage*, *40*(2), 869–883.

Stroop, J. (1935). Studies of interference in serial verbal reaction. *Journal of Experimental Psychology*, *18*, 643–662.

Sturz, B. R., Green, M. L., Locker Jr, L., & Boyer, T. W. (2013). Stroop interference in a delayed match-to-sample task: Evidence for semantic competition. *Frontiers in Psychology*, *4*.

Sundermann, B., & Pfleiderer, B. (2012). Functional connectivity profile of the human inferior frontal junction: Involvement in a cognitive control network. *BMC Neuroscience*, *13*(1), 119.

Swann, N. C., Cai, W., Conner, C. R., Pieters, T. A., Claffey, M. P., George, J. S., ... Tandon, N. (2012). Roles for the pre-supplementary motor area and the right inferior frontal gyrus in stopping action: Electrophysiological responses and functional and structural connectivity. *NeuroImage*, *59*(3), 2860–2870.

Szűcs, D., & Csépe, V. (2004). Access to numerical information is dependent on the modality of stimulus presentation in mental addition: A combined ERP and behavioral study. *Cognitive Brain Research*, *19*(1), 10–27.

Szűcs, D., & Soltész, F. (2012). Functional definition of the N450 event-related brain potential marker of conflict processing: A numerical Stroop study. *BMC Neuroscience*, *13*(1), 35-38.

Tang, J., Critchley, H., Glaser, D., Dolan, R., & Butterworth, B. (2006). Imaging informational conflict: A functional magnetic resonance imaging study of Numerical Stroop. *Journal of Cognitive Neuroscience*, *18*(12), 2049–2062.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, *94*(26), 14792–14797.

Treisman, A. M. (1998). Feature binding, attention and object perception. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *353*(1373), 1295–1306.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive psychology*, *12*(1), 97–136.

Trick, L. M., & Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychological Review*, *101*(1), 80.

Uddin, L. Q., Supekar, K. S., Ryali, S., & Menon, V. (2011). Dynamic reconfiguration of structural and functional connectivity across core neurocognitive brain networks with development. *The Journal of Neuroscience*, *31*(50), 18578–18589.

Van Maanen, L., & Van Rijn, H. (2008). The Picture-Word Interference effect is a Stroop effect after all. In *Proceedings of the 30th annual meeting of the cognitive science society* (pp. 645–650).

Van Maanen, L., Van Rijn, H., & Borst, J. P. (2009). Stroop and Picture-Word Interference are two sides of the same coin. *Psychonomic Bulletin and Review*, *16*(6), 987–999.

Van Opstal, F., & Verguts, T. (2011). The origins of the numerical distance effect: The same–different task. *Journal of Cognitive Psychology*, *23*(1), 112–120.

Venkatraman, V., Rosati, A. G., Taren, A. A., & Huettel, S. A. (2009). Resolving response, decision, and strategic control: Evidence for a functional topography in dorsomedial prefrontal cortex. *The Journal of Neuroscience*, *29*(42), 13158–13164.

Vetter, P., Butterworth, B., & Bahrami, B. (2011). A candidate for the attentional bottleneck: Set-size specific modulation of the right TPJ during attentive enumeration. *Journal of Cognitive Neuroscience*, *23*(3), 728–736.

Vigliocco, G., Antonini, T., & Garrett, M. F. (1997). Grammatical gender is on the tip of Italian tongues. *Psychological science*, *8*(4), 314–317.

Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*(6), 3328–3342.

Vuokko, E., Niemivirta, M., & Helenius, P. (2013). Cortical activation patterns during subitizing and counting. *Brain Research*, 40–52.

Wessel, J. R., Danielmeier, C., Morton, J. B., & Ullsperger, M. (2012). Surprise and error: common neuronal architecture for the processing of errors and novelty. *The Journal of Neuroscience*, *32*(22), 7528–7537.

Wiefel, A., Pauen, S., & Dueck, M. (2009). Do infants count like scientists? *Behavioral and Brain Sciences*, *32*(3-4), 355–356.

Wong, B., & Szűcs, D. (2013). Single-digit arabic numbers do not automatically activate magnitude representations in adults or in children: Evidence from the symbolic same–different task. *Acta Psychologica*, *144*(3), 488–498.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, *358*(6389), 749–750.

Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., & Courtney, S. M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience*, *5*(10), 995–1002.

Zachariou, V., Nikas, C. V., Safiullah, Z. N., Behrmann, M., Klatzky, R., & Ungerleider, L. G. (2015). Common dorsal stream substrates for the mapping of surface texture to object parts and visual spatial processing. *Journal of Cognitive Neuroscience*, *27*(12), 2442-2461.

Zarahn, E., Aguirre, G., & D'Esposito, M. (1997). A trial-based experimental design for fMRI. *NeuroImage*, *6*(2), 122–138.

Zhang, H., & Kornblum, S. (1998). The effects of stimulus–response mapping and irrelevant stimulus–response and stimulus–stimulus overlap in four-choice Stroop tasks with single-carrier stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(1), 3–19.

Zhou, X., Chen, C., Dong, Q., Zhang, H., Chen, C., Qiao, S., ... Guo, Y. (2006). Numerical distance effect in the N240 component in a number-matching task. *Neuroreport*, *17*(10), 991–994.

Zysset, S., Müller, K., Lohmann, G., & von Cramon, D. Y. (2001). Color-word matching Stroop task: Separating interference and response conflict. *NeuroImage*, *13*(1), 29–36.

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Appendix A

APPENDIX

A.1 Stimulus Material

A.1.1 Picture Word Interference Task, Set A

Table A.1: Pilot I, stimulus material set A, Picture Word Interference Task, english version in brackets

picture	distractor related	distractor unrelated	distractor same
Ananas (pineapple)	Mango (mango) Kiwi (kiwi)	Kissen (pillow) Boot (boat)	Ananas
Auto (car)	Bus (bus) Lkw (truck)	Bär (bear) Quitte (quince)	Auto
Baum (tree)	Gras (grass) Strauch (shrub)	Echse (lizard) Finger (finger)	Baum
Bein (leg)	Arm (arm) Knie (knee)	Knoblauch (gralic) Dübel (wall plug)	Bein
Bett (bed)	Kissen (pillow) Sofa (couch)	Arm (arm) Hummel (bumble bee)	Bett
Birne (pear)	Quitte (quince) Aprikose (apricot)	Nebel (fog) Gans (goose)	Birne
Brot (bread)	Kuchen (cake) Keks (cookie)	Schraube (screw) Kiwi (kiwi)	Brot
Drachen (kite)	Segel (sail) Ballon (baloon)	Banane (banana) Feige (fig)	Drachen
Erdbeere (strawberry)	Banane (banana) Feige (fig)	Pokal (cup / trophy) Pullover (pullover)	Erdbeere
Esel (donkey)	Kuh (cow) Zebra (zebra)	Bluse (blouse) Kappe (cap)	Esel
Fisch (fish)	Qualle (jellyfish) Muschel (shell)	Bohrer (driller) Zebra (zebra)	Fisch
Flasche (bottle)	Karaffe (decanter) Kanne (jug)	Asteroid (asteroid) Schnee (snow)	Flasche
Fliege (fly)	Mücke (mosquito) Hummel (bumble bee)	Hammer (hammer) Karaffe (decanter)	Fliege
Flugzeug (airplane)	Boot (boat) Schiff (ship)	Ente (duck) Radieschen (radish)	Flugzeug
Glas (glass)	Tasse (cup) Becher (mug)	Knöchel (ankle) Schrank (cupboard)	Glas
Hand (hand)	Knöchel (ankle) Finger (finger)	Wolf (wulf) Muschel (shell)	Hand
Harfe (harp)	Cello (cello) Geige (violin)	Mücke (mosquito) Sonne (sun)	Harfe
Hemd (shirt)	Bluse (blouse)	Kuchen (cake)	Hemd

	Pullover (pullover)	Kanne (jug)	
Hund (dog)	Wolf (wulf)	Mango (mango)	Hund
	Schakal (jackal)	Gewehr (rifle)	
Hut (hat)	Kappe (cap)	Schakal (jackal)	Hut
	Mütze (cap/beanie)	Segel (sail)	
Kanone (cannon)	Gewehr (rifle)	Lkw (truck)	Kanone
	Pistole (gun)	Tasse (cup)	
Mond (moon)	Asteroid (asteroid)	Kuh (cow)	Mond
	Sonne (sun)	Strauch (shrub)	
Nagel (nail)	Schraube (screw)	Posaune (trombone)	Nagel
	Dübel (wall plug)	Wurm (worm)	
Nashorn (rhino)	Giraffe (girafe)	Mütze (cap)	Nashorn
	Bär (bear)	Aprikose (apricot)	
Säge (saw)	Bohrer (driller)	Cello (cello)	Säge
	Hammer (hammer)	Becher (mug)	
Schildkröte (turtle)	Echse (lizard)	Keks (cookie)	Schildkröte
	Leguan (iguana)	Pistole (gun)	
Schnecke (snail)	Raupe (caterpillar)	Bus (bus)	Schnecke
	Wurm (worm)	Ballon (baloon)	
Schwan (swan)	Ente (duck)	Regal (shelve)	Schwan
	Gans (goose)	Urne (urn)	
Tisch (table)	Regal (shelve)	Raupe (caterpillar)	Tisch
	Schrank (cupboard)	Saxophon (saxophone)	
Trompete (trumpet)	Posaune (trombone)	Giraffe (girafe)	Trompete
	Saxophon (saxophone)	Leguan (iguana)	
Vase (vase)	Urne (urn)	Qualle (jellyfish)	Vase
	Pokal (cup / trophy)	Knie (knee)	
Wolke (cloud)	Nebel (fog)	Schiff (ship)	Wolke
	Schnee (snow)	Geige (violin)	
Zwiebel (onion)	Knoblauch (garlic)	Gras (grass)	Zwiebel
	Radieschen (radish)	Sofa (couch)	

A.1.2 Picture Word Interference Task, Set B

Table A.2: Pilot I, stimulus material set B, Picture Word Interference Task, english version in brackets. All items marked with asterix (*) were also used in the fMRI experiment.

picture	distractor related	distractor unrelated	distractor same
Adler (eagle)/ Pfau (peacock)*	Geier (vulture)	Zange (pliers)	Adler/ Pfau
	Falke (falcon)	Brombeere (blackberry)	
Ameise (ant)*	Biene (bee)	Schlagzeug (drumset)	Ameise
	Wespe (wasp)	Schal (scarf)	
Apfel (apple)*	Zwetschge (plum)	Oboe (oboe)	Apfel
	Brombeere (blackberry)	Deckel (lid)	
Blume (flower)*	Hecke (hedge)	Pony (pony)	Blume
	Kraut (herb/ cabbage)	Fasan (pheasant)	
Elefant (elephant)*	Nilpferd (rhinoceros)	Nektarine (nectarine)	Elefant
	Mammut (mammoth)	Füller (fountainpen)	
Flöte (flute)*	Oboe (oboe)	Gecko (gecko)	Flöte
	Klarinette (clarinet)	Kraut (herb/cabbage)	
Fuchs (fox)*	Dachs (badger)	Mandarine (mandarine)	Fuchs
	Hyäne (hyena)	Synagoge (synagogue)	
Huhn (chicken)*	Fasan (pheasant)	Zwetschge (plum)	Huhn
	Pfau (peacock)	Mirabelle (yellow plum)	
Hummer (lobster)*	Krebs (crab)	Kohl (cabbage)	Hummer

	Krabbe (shrimp)	Rhabarber (rhubarb)	
Kirche (church)*	Moschee (mosque)	Tablett (tray)	Kirche
	Synagoge (synagogue)	Hamster (hamster)	
Kirsche (cherry)*	Himbeere (raspberry)	Zigarette (cigarette)	Kirsche
	Pflaume (plum)	Grille (cricket)	
Kleid (dress)*	Rock (skirt)	Auge (eye)	Kleid
	Hose (trousers/ pants)	Schlange (snake)	
Krokodil (crocodile)*	Gecko (gecko)	Pauke (kettle drum)	Krokodil
	Schlange (snake)	Weizen (wheat)	
Löffel (spoon)*	Kelle (scoop)	Nilpferd (hippopotamus)	Löffel
	Sieb (sieve)	Biene (bee)	
Mais (corn)*	Weizen (wheat)	Hocker (stool)	Mais
	Gerste (barley)	Teller (plate)	
Mantel (coat)*	Jacke (jacket)	Ziege (goat)	Mantel
	Schal (scarf)	Sieb (sieve)	
Maus (mouse)*	Ratte (rat)	Himbeere (raspberry)	Maus
	Hamster (hamster)	Pflaume (plum)	
Ohr (ear)*	Auge (eye)	Topf (pot)	Ohr
	Mund (mouth)	Feile (file)	
Pfanne (pan)*	Topf (pot)	Geier (vulture)	Pfanne
	Deckel (lid)	Hyäne (hyena)	
Pfeife (pipe)*	Zigarette (cigarette)	Käfer (bug)	Pfeife
	Zigarre (cigar)	Tanker (tanker ship)	
Pfirsich (peach)/ Birne (pear)*	Nektarine (nectarine)	Dachs (badger)	Pfirsich/ Birne
	Mirabelle (yellow plum)	Falke (falcon)	
Pinsel (brush)*	Stift (pen)	Zwetschge (plum)	Pinsel
	Füller (fountainpen)	Gurke (cucumber)	
Salat (salad)*	Kohl (cabbage)	Fähre (ferry)	Salat
	Gurke (cucumber)	Mund (mouth)	
Schaf (sheep)*	Ziege (goat)	Fähre (ferry)	Schaf
	Pony (pony)	Mund (mouth)	
Schere (scissors)*	Zange (pliers)	Ratte (rat)	Schere
	Feile (file)	Gerste (barley)	
Spargel (asparagus)*	Lauch (leek)	Wepse (wasp)	Spargel
	Rhabarber (rhubarb)	Mammut (mammoth)	
Spinne (spider)*	Grille (cricket (insect))	Orange (orange)	Spinne
	Käfer (bug)	Rock (skirt)	
Stern (star)*	Planet (planet)	Krebs (crab)	Stern
	Komet (comet)	Couch (couch/ sofa)	
Stuhl (chair)*	Hocker (stool)	Lauch (leek)	Stuhl
	Couch (couch/ sofa)	Klarinette (clarinet)	
Trommel (drum)*	Pauke (kettledrum)	Hose (trousers/ pants)	Trommel
	Schlagzeug (drumset)	Planet (planet)	
Zitrone (lemon)*	Mandarine (mandarine)	Jacke (jacket)	Zitrone
	Orange (orange)	Pfau (peacock)	
Zug (train)*	Fähre (ferry)	Krabbe (crab)	Zug
	Tanker (tanker ship)	Hecke (hedge)	

Table A.3: Six temporal variations of the PWI and NSP fMRI trials.

trial timing						
jitter number	#1	#2	#3	#4	#5	#6
fixation cross presentation time	0	0	0	0	0	0
fixation cross duration	500	500	500	500	500	500
blank screen time	500	500	500	500	500	500
blank screen duration	2000	1500	1000	500	2000	1500
stimulus onset	2500	2000	1500	1000	2500	2000
stimulus duration	500	500	500	500	500	500
blank screen time	3000	2500	2000	1500	3000	2500
blank screen duration	5000	4500	4000	3500	5500	4500
cue onset	8000	7000	6000	5000	8500	7000
cue duration	2000	2000	2000	2000	2000	2000
blank screen onset	10000	9000	8000	7000	10500	9000
blank screen duration	2000	3000	4000	5000	1500	3000
trial duration in total:	12000	12000	12000	12000	12000	12000

The **two critical time periods** (stimulus presentation and cue presentation) are highlighted in bold.
Jittered parts of the trial design are stressed in italic.

Table A.4: Mutual neural network for task and response in the Numerical Stroop task.

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
(Task + Response) > baseline					
Left transverse temporal gyrus or Heschl's gyrus (42)	-62	-12	8	6.07	823
	-50	-14	18	5.00	
	-58	8	0	4.85	
Right transverse temporal gyrus or Heschl's gyrus (42)	66	-10	8	5.93	183
Right postcentral gyrus (3)	54	-8	52	4.28	121
	46	-12	58	3.98	
	64	-10	36	3.96	

Numerical Stroop task conjunction performed on whole-brain results post stimulus onset ('task') and post cue onset ('response') against implicit baseline. MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < .05$, with a minimum cluster extend of $k > 100$ derived with $p < .001$. Labelling was provided by the Anatomy toolbox (Eickhoff et al., 2005), Brodmann areas in parentheses.

Table A.5: Mutual neural network for task and response in the Picture Word Interference task.

Anatomic Localization (Brodmann area)	Peak MNI Coordinates x	y	z	t	Cluster
(Task + Response) > baseline					
Right Rolandic Operculum and (43)	64	-6	8	8.41	2008
postcentral gyrus	66	-4	24	7.89	
	52	-8	22	6.33	
Left Rolandic Operculum and (43)	-64	-4	10	7.64	1965
postcentral gyrus	-64	-12	34	5.87	
	-50	-10	54	5.64	

Picture Word Interference paradigm conjunction performed on whole-brain results post stimulus onset ('task') and post cue onset ('response') against implicit baseline. MNI coordinates derived from T-maps with $T > 3.17$, at a cluster-corrected significance threshold of $p < .05$, with a minimum cluster extend of $k > 97$ derived with $p < .001$. Labelling was provided by the Anatomy toolbox (Eickhoff et al., 2005), Brodmann areas in parentheses.

Nomenclature

ALE	activation likelihood estimation
BA	Brodmann area
BG	basal ganglia
DLPFC	dorsolateral prefrontal cortex
ERP	event-related potential
fNIRS	functional near-infrared spectroscopy
FPCS	fronto-parietal control system
hIPS	horizontal segment of the intraparietal sulcus
IFJ	inferior frontal junction
LGN	lateral geniculate nucleus
LOC	lateral occipital cortex
LSC	lexical selection by competition
MEG	magnetoencephalography
MVPA	multi-voxel pattern analysis
NDE	numerical distance effect
NSP	Numerical Stroop task
PAC	primary auditory cortex
PET	positron emission tomography
PPI	Picture-Picture Interference paradigm
PRC	perirhinal cortex
PWI	Picture-Word Interference task
RT	reaction time
SMA	supplementary motor area
SNARC	spatial-numerical association of response codes
SPL	superior parietal lobe
STM	short-term memory
TFR	time-frequency representations
TMS	transcranial magnetic stimulation
VLPFC	ventrolateral prefrontal cortex
WM	working memory